Influence of oceanographic environment on the distribution and condition of yellowtail kingfish (*Seriola lalandi*) within a climate change hotspot

Curtis Champion

B.Env.Sc. (Hon Class 1)

Institute for Marine and Antarctic Studies

University of Tasmania

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- Statement of co-authorship -

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

Candidate: Curtis Champion, Institute for Marine and Antarctic Studies, University of Tasmania

Author 1: Alistair Hobday, CSIRO Oceans and Atmosphere

Author 2: Gretta Pecl, Institute for Marine and Antarctic Studies, University of Tasmania

Author 3: Sean Tracey, Institute for Marine and Antarctic Studies, University of Tasmania

Author 4: Xuebin Zhang, CSIRO Oceans and Atmosphere

Chapter 2 (Paper 1)

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Curtis Champion collated species occurrence records, developed models, undertook statistical analyses, developed and plotted spatial projections and undertook 90% of the manuscript preparation. Alistair Hobday extracted oceanographic data, matched species occurrence records with oceanographic variables and constructively edited the manuscript. Gretta Pecl and Sean Tracey constructively edited the manuscript and suggested data presentations options.

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Curtis Champion collated species occurrence records, developed models, undertook statistical analyses, developed and plotted spatial projections and undertook 90% of the manuscript preparation. Alistair Hobday extracted oceanographic data, matched species occurrence records with oceanographic variables and constructively edited the manuscript. Xuebin Zhang provided modelled future oceanographic data and drafted the methods section relating to modelling physical oceanographic variables. Gretta Pecl and Sean Tracey constructively edited the manuscript and suggested data presentations options.

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Curtis Champion collected field samples, ran experiments, undertook statistical analyses, plotted the data and undertook 90% of the manuscript preparation. Alistair Hobday provided access to the bioelectrical impedance analysis tool, suggested factors to experimentally measure and constructively edited the manuscript. Sean Tracey aided in fieldwork planning, collected field samples and constructively edited the manuscript. Gretta Pecl refined the study scope and constructively edited the manuscript.

Chapter 5 (Paper 4)

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Curtis Champion collected field data, developed models, undertook statistical analyses, plotted the data and undertook 90% of the manuscript preparation. Alistair Hobday provided access to the bioelectrical impedance analysis tool, extracted oceanographic data and constructively edited the manuscript. Sean Tracey collected field data and constructively edited the manuscript. Gretta Pecl refined the study's scope and constructively edited the manuscript.

We, the undersigned, endorse the above stated contribution of work undertaken for each of the published (or submitted) peer-reviewed manuscripts contributing to this thesis:

Curtis Champion	Sean Tracey	Caleb Gardener
Candidate	*Primary Supervisor*	*Head of School*
Institute for Marine and Antarctic Studies	Institute for Marine and Antarctic Studies	Institute for Marine and Antarctic Studies
University of Tasmania	University of Tasmania	University of Tasmania
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- Thesis abstract -

Preferences for environmental conditions fundamentally underpin species' distributions and ecologies. However, shifts in environmental conditions that are consistent with the effects of climate change are increasingly exposing species to conditions that are outside their preferred climate envelope. In response, marine species and communities globally have been affected through changes in 1. geographic distribution, 2. species phenology, 3. ecological interactions and 4. ecosystem structure and dynamics. Although biological responses to environmental change challenges future conservation planning and fisheries management, measured relationships between the environment and ecology for marine species can underpin proactive climate adaptation. This thesis examines the effects of seasonal and longer-term climate-driven oceanographic change on the distribution and body condition of a model coastal-pelagic species, yellowtail kingfish (*Seriola lalandi*; hereafter 'kingfish'), throughout its eastern Australian distribution. This region is among the most rapidly warming areas of the global ocean, and is used within this thesis as a natural laboratory and early learning location for quantifying and projecting relationships between the environment, distribution and condition of kingfish.

Assessing historical biological responses to environmental change and predicting the future effects of continued global change requires an understanding of species' environmental habitat preferences. Species distribution, or habitat suitability, models provide a framework for quantifying species' responses to a suite of environmental variables and for projecting environmental habitat preferences spatially. Here, a habitat model for kingfish from eastern Australia is developed using citizen science data and remotely sensed environmental covariates to assess for historic ('historic analysis') and future ('future analysis') climate-driven changes

in the distribution of suitable oceanographic habitat. The optimal model for kingfish oceanographic habitat contained the predictors sea surface temperature, sea level anomaly and eddy kinetic energy, demonstrating that the distribution of kingfish from eastern Australia is driven by simultaneous responses to multiple oceanographic factors.

The historical analysis encompassed a 22-year period from 1996 to 2017 and revealed that rapid poleward shifts in the core (94.4 km/decade) and poleward edge (108.8 km/decade) of kingfish oceanographic habitat have occurred off eastern Australia over this period. This analysis accounted for the effects of natural intra- and interannual climate variability, suggesting that the rate and magnitude of these distributional shifts is likely due to human-induced environmental change. These methods and results demonstrate the utility of marine citizen science data for quantifying climate-driven redistributions, but necessitates shifting focus from species distributions directly, to the distribution of species' environmental habitat preferences.

The future analysis used dynamically downscaled oceanographic variables to assess for changes in the temporal persistence (months per year) of suitable kingfish oceanographic habitat within south-eastern Australia's six coastal bioregions between 1996 and 2040. This analysis identified that a decline in temporal habitat persistence is predicted for the northernmost (equatorward) bioregion, whereas increases are predicted for the three southernmost (poleward) bioregions. Furthermore, temporal habitat persistence is shown to be an important metric for potential climate change adaptation, particularly when predicted at near-term decision-making time-scales, because it provides fishery-relevant information (i.e. a measure of fishing opportunity). This analysis demonstrates how novel metrics relevant to climate adaptation can be derived from projections of species' environmental habitats, and are

appropriate for the management of fisheries resources and protection of high conservation value species under future climate change.

While habitat models are commonly used to estimate a species' probability of occurrence, they have not been used to examine the effect of environmental habitat suitability on fish condition, which is considered to be an integrated measure of physiological status. Bioelectrical impedance analysis (BIA) has emerged as a rapid, nonlethal and cost-effective method for measuring fish condition and can provide data that are suitable for comparison with habitat models. While BIA has a history of application in medical fields, it is a relatively novel tool in fish and fisheries research requiring consideration of potential sources of error to ensure robust and comparable data are obtained. In light of this, the effects of five factors related to fish handling on an instantaneous body condition index (phase angle) were experimentally tested. These experiments identified significant effects of time since death, temperature of the tissue, removal of the gills and gastrointestinal tract, and the anatomic location for measurements on BIA measurements. Results were used to develop a protocol for the field-based application of BIA to control for potential measurement error associated with variable fish handling procedures.

Adhering to the aforementioned protocol, the body condition of 113 kingfish from south-eastern Australia were measured using BIA over three consecutive austral summer–autumn periods (2016/17–2018/19). These data were compared to modelled oceanographic habitat to 1. test whether individuals sampled from areas of high-quality habitat were in better condition than individuals sampled from areas of low-quality habitat, and 2. assess whether the condition of kingfish responded to oceanographic habitat suitability predicted at varying time-before-capture periods. Oceanographic habitat suitability was found to be significantly correlated with

kingfish condition at time-before-capture periods ranging from one to four weeks and became increasingly correlated at shorter lead-times. These results highlight that 1. fish condition can respond sensitively to environmental variability and this response can be detected using oceanographic habitat suitability models, and 2. climate change may drive extensions in species range limits through spatial shifts in oceanographic habitat quality that allow individuals to persist beyond historical range boundaries without their body condition being compromised.

The results of this thesis emphasise that strong relationships can exist between the environment, distribution and condition of pelagic fishes. This body of evidence highlights the value of environmental variables as proxies for the distribution and condition of pelagic fishes and supports climate change adaptation strategies that are underpinned by correlative species-environment relationships. However, it remains considerably uncertain whether known biological responses to environmental variables can be extrapolated to novel regions or time periods. Transferability is a particularly important consideration when using established relationships between species and their environment to forecast the future ecological effects of climate change and develop adaptation strategies. Where data allows, a mechanistic understanding of species responses to environmental variables should be considered alongside correlative relationships to improve the robustness of species-environment relationships to the novel environmental conditions that biodiversity will inevitably face in a rapidly changing world.

- Chapter 1 – Introduction -

Species responses to environmental conditions fundamentally underpin their distributions and ecologies (Grinnell 1904; Guisan and Zimmermann 2000; Hutchinson 1957; Pearson and Dawson 2003). This is especially true for marine ectotherms due to their reliance on environmental temperature to regulate physiological processes (Pinsky *et al.* 2019; Sunday *et al.* 2012). Subsequently, relationships between species and environmental variables are valuable for predicting species distributions (Elith and Leathwick 2009), and form the cornerstone of the field of species distribution modelling (Araujo and Guisan 2006; Guisan and Zimmermann 2000). Environmental variables may also be useful for predicting how physiological indices in marine ectotherms, such as body condition (Champion *et al.* 2019a), growth and reproduction, vary within populations through space and time, however there remains a paucity of quantitative comparisons. While biotic interactions are also important determinants of the realised distributions and ecologies of species (Araújo and Luoto 2007; Guisan *et al.* 2006), these are dependent on the convergence of environmental conditions that are tolerable by multiple interacting species (Godsoe and Harmon 2012). Therefore, environmental habitat preferences can provide valuable estimates of where and when species will occur and their likelihood of forming viable populations in spatially explicit domains (Hutchinson 1957; Soberon and Peterson 2005).

Quantifying species' preferences for environmental conditions has broad practical utility, including for adaptive fisheries and aquaculture management (Hobday *et al.* 2016c), assessing biosecurity risk (Sutherst 2014) and for strategic conservation planning (Leathwick *et al.* 2008; Maxwell *et al.* 2009). For example, the thermal habitat preference of the iconic loggerhead sea turtle (*Caretta caretta*) has been used to help Hawaii-based pelagic longline fishers to identify

oceanographic environments that minimise rates of turtle bycatch (Howell *et al.* 2008). In the past decade research utilising relationships between species and environmental conditions has rapidly increased due to a growing understanding of the environmental effects of contemporary climate change (Bonebrake *et al.* 2018). For example, climate change attribution studies commonly draw upon correlations between species and their environments to hindcast biological change (e.g. shifts in species distributions; Hill *et al*. 2015), while modelled projections of environmental conditions are used to forecast future change (Hobday 2010) and consider human adaptation options (Champion *et al.* 2019b). The rapid and pervasive effects of contemporary climate change on global biodiversity (Pecl *et al.* 2017) highlights the urgent need to respond, and species-environmental relationships provide a pragmatic approach for rapidly progressing climate impact attribution and adaptation science. Research motivated by the need to understand the biological effects of climate change also provides an opportunity to better understand how species physiologies and ecologies are shaped by their environment, which has a long history in ecology (Darwin 1859) and remains a research frontier (Payne and Smith 2016; Pinsky *et al.* 2019; Sunday *et al.* 2015).

1.1 – Climate-driven environmental change in marine systems

Throughout evolutionary history species have been exposed to natural variation in environmental conditions over seasonal and interannual time-scales. However, unprecedented shifts in environmental conditions that exceed the rate and magnitude of natural climate variation are now evident throughout the global ocean (IPCC 2018). These changes are consistent with the effects of increased atmospheric concentrations of greenhouse gasses and include rising ocean temperatures, ocean acidification, increasing frequency and intensity of extreme events and alteration of ocean current velocity, mixed layer depth and water column

stratification (IPCC 2018). It is highly probable that the sustained and ongoing emission of greenhouse gases, combined with the long residence time of these compounds in the atmosphere, will drive a continuation of these changes into the future (Solomon *et al.* 2009). Given that the environmental effects of climate change are indiscriminate and occur over large spatial extents, and that the global ocean encompasses 71% of the earth's surface, marine environments are broadly exposed to the effects of climate change. However, different regions of the global ocean are known to vary in their degree of climate change exposure (Hobday and Pecl 2014), presenting an opportunity for strategically prioritising climate change impact and adaptation research (Pecl *et al.* 2014b), but challenging the broad applicability of results obtained from disparate regions.

1.1.1 – South-eastern Australia: A marine climate change hotspot

Effects of climate change on the oceanography of south-eastern Australia is not a future prospect but rather a present reality. Ocean warming in this region is primarily attributed to the poleward extension of the southward flowing East Australian Current (EAC) in response to climate change induced increases in wind stress over high-latitude regions of the South Pacific Ocean (Cai *et al.* 2005; Sloyan and O'Kane 2015). Subsequently, coastal and pelagic environments adjacent to south-eastern Australia are warming at a rate that is between 3 and 4 times more rapid than the global average (Ridgway 2007), placing this region among the top 10% of fastest warming areas of the global ocean (Hobday and Pecl 2014). Analyses of remotely sensed sea surface temperature for Australia confirm the rapid nature of marine warming in this region. For example, comparisons between five-year seasonally averaged sea surface temperature measurements between 1996 and 2016 highlight rates of change in excess of 2°C over this period (Figure 1.1). Furthermore, the magnitude of sea surface temperature

increase off south-eastern Australia between 1996 – 2016 was greater during summer than winter (Figure 1.1), which may compromise the physiology of species that exist close to their upper thermal limits during the warmest months of the year (Payne *et al.* 2016).

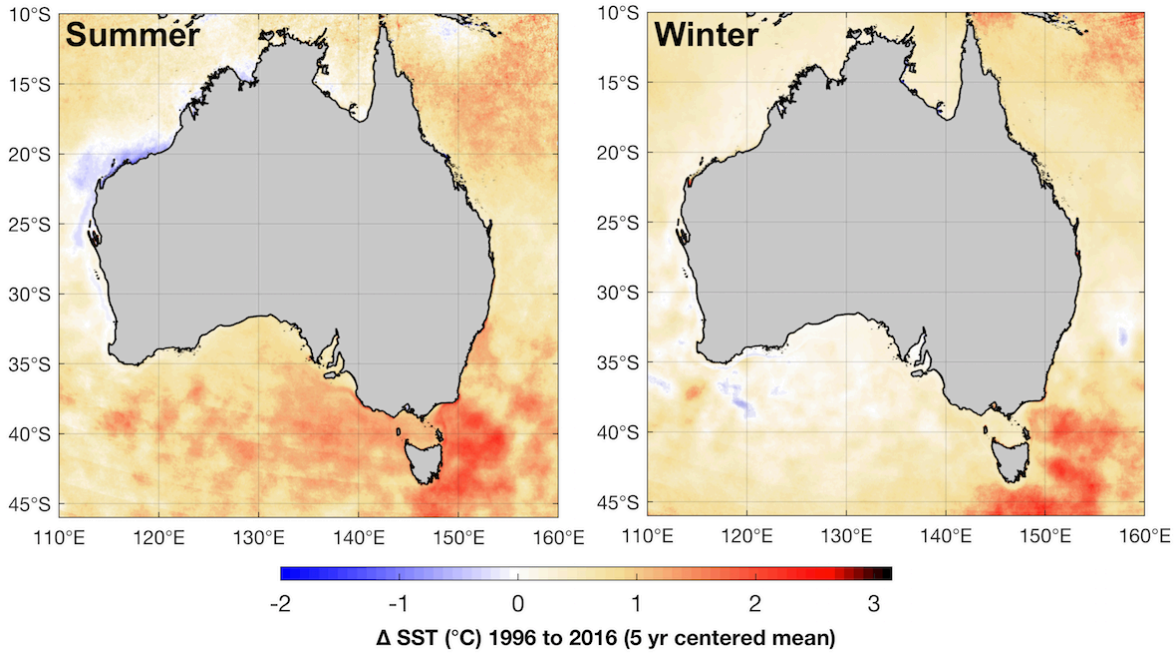

Figure 1.1. Observed summer (December – February) and winter (June – August) sea surface temperature change for Australia between 1996 and 2016. Changes in degrees Celsius are based on comparisons of 5-year averages centred on 1996 and 2016. Data used: CSIRO SST 3-day composite.

Historical climate-driven changes in oceanographic variables other than sea surface temperature and the velocity of the EAC are less clear in south-eastern Australia. However, an increase in seawater salinity over the 1944 – 2002 period has been identified for eastern Tasmania (Ridgway 2007) and a reduction of surface ocean pH by approximately 0.1 units since the industrial revolution has been reported at a global scale (Feely *et al.* 2004; Sabine *et al.* 2004). Marine heatwave events (Hobday *et al.* 2016a) are also increasingly affecting marine systems by becoming more frequent and persisting for longer due to climate change (Oliver *et al.* 2018). Global analyses have shown that the number of marine heatwave days per year has

doubled since 1982 (Frölicher *et al.* 2018). Findings from south-eastern Australia concur with these global trends. For example, Oliver *et al.* (2017) highlighted that the 2015/16 Tasman Sea marine heatwave was the longest (9.11.15 to 16.5.16) and most intense recorded in the region since satellite records began in 1982. This extreme event was found to be approximately 6.8 times more likely to have occurred due to the influence of anthropogenic climate change (Oliver *et al.* 2017).

Future projections for south-eastern Australia's marine environment indicate that climate change will continue to alter marine environmental variables at rates that are likely to exceed changes that have already been recorded (Hobday and Lough 2011). The continued warming of south-eastern Australia's marine environment is projected to be driven by further poleward advances of the EAC over the coming century, with a 20% increase in mean flow predicted by 2070 (Cai *et al.* 2005). By 2050, average sea surface temperatures off south-eastern Australia are projected to be at least 2°C higher for all months of the year relative to the 1990–2000 average (Hobday and Lough 2011). Ocean warming is also likely to be compounded by increasing solar radiation at the ocean's surface under climate change (Hobday and Lough 2011). These concurrent environmental effects suggest that south-eastern Australia's marine environment will remain a globally important hotspot of climate change into the foreseeable future (Pecl *et al.* 2014b).

1.2 – Biological responses to marine environmental change

As climate change alters environmental conditions beyond the climate envelope that species are adapted to, marine biological systems can respond through changes to (Walther *et al.* 2002):

1. *species phenology and physiology*; for example, the timing of spawning events (Edwards and Richardson 2004) or species tolerance to increased water temperatures (Crozier and Hutchings 2014; Donelson *et al.* 2011).

2. *species distributions*; for example, shifts in the spatial distribution of marine fishes in order to track changes in preferred environmental conditions (Sunday *et al.* 2015).

3. *composition and interactions within ecosystems*; for example, the climate driven arrival of range extending herbivores can drive declines in key habitat forming species that support valuable fisheries (Ling *et al.* 2009; Vergés *et al.* 2016).

4. *structure and dynamics of communities*, including changes in ocean productivity in response to physical environmental changes and associated flow-on effects to marine food webs (Brown *et al.* 2010).

Of these key biological responses to climate-driven environmental change, species redistributions, or range shifts, have been most widely documented (Pecl *et al.* 2017; Pinsky *et al.* 2013; Poloczanska *et al.* 2013) and are associated with well-developed explanatory theories of how and why range shifts occur (Bates *et al.* 2014) and how future species redistribution may proceed under climate change (Urban *et al.* 2016). This has led Bonebrake *et al.* (2018) to consider the ecology of species redistribution under two broad and complementary areas: explanatory ecology and anticipatory ecology. Explanatory ecology generally aims to evaluate models and theory to enhance scientific understanding of the processes that drive species redistribution, while anticipatory ecology intends to forecast parameters likely to be impacted

by anthropogenic factors in order to predict the biological effects of climate change (Bonebrake *et al.* 2018). Data chapters contained within this thesis follow this broad dichotomy, where chapters Two and Five are characteristic of explanatory species redistribution science, while chapter Three can be characterised as anticipatory species redistribution science.

While a diverse suite of marine taxa are responding to changing environmental condition through shifts in distribution (reef associated fishes: (Figueira and Booth 2010), pelagic fishes: (Worm and Tittensor 2011), cephalopods: (Ramos *et al.* 2018), gastropods: (Nimbs *et al.* 2016), macroalgae: (Wernberg *et al.* 2011)), the rate and magnitude of climate-driven range shifts are highly variable. Variation in biological responses to climate change is likely to reflect differences in the exposure of marine species to physical change and/or varying sensitivity to changing environmental conditions (Pecl *et al.* 2014c). Research undertaken in eastern Australia shows that rates of climate-driven range change in pelagic fishes that associate with dynamic oceanographic variables markedly exceed rates of change reported for near-shore and reef-associated fishes (Champion *et al.* 2018a; Hill *et al.* 2015; Hobday 2010; Stuart-Smith *et al.* 2010; Sunday *et al.* 2015). Furthermore, traits common to pelagic species, including high adult mobility and broad latitudinal range size, are known to correlate with high rates of range extensions (Sunday *et al.* 2015). These findings indicate that coastal-pelagic fishes are broadly exposed to the oceanographic effects of climate change, are likely to be sensitive to environmental heterogeneity and have the capacity through mobility to respond to environmental change through shifts in distribution. These attributes present challenges for the sustainability of coastal-pelagic fish stocks and threaten the viability of fisheries that target these species. Therefore, anticipatory climate adaptation research on coastal-pelagic fishes should be prioritised in order to minimises losses and capitalise on future opportunities.

1.4 – Study species

The yellowtail kingfish *Seriola lalandi* (hereafter "kingfish") is a coastal-pelagic species extending along the southern coast of mainland Australia (Gillanders *et al.* 2001; Hobday and Campbell 2009). Kingfish are a popular and high-value target species in eastern Australian fisheries, where the estimated annual recreational catch exceeds the average annual commercial catch (Henry and Lyle 2003; Lowry *et al.* 2016). Kingfish from south-eastern Australia and New Zealand form a single genetically distinct population (Miller *et al.* 2011). A significant proportion of individuals from this population originate from waters surrounding Lord Howe Island and Elizabeth and Middleton reefs (i.e. central Tasman Sea) (Patterson and Swearer 2008). While some individuals have been documented moving large distances (Brodie 2015; Gillanders *et al.* 2001), tag-recapture (Gillanders *et al.* 2001) and acoustic telemetry (Brodie 2015) methods have demonstrated that the majority of individuals typically move less than 50 km over seasonal time-scales.

Recently, photo-verified observations of kingfish approximately 200 km poleward of the previous southernmost occurrence record for this species have been reported by anglers and recorded by the Range Extension Database and Mapping Project (Redmap; www.redmap.org.au; Stuart-Smith *et al.* 2016). These observations provide considerable evidence for the detection of kingfish outside of its historical range, but low confidence in the historical range boundary for kingfish has resulted in overall low confidence of this species undergoing a range extension (Robinson *et al.* 2015a). Nevertheless, observations of fishes outside their usual distributions can be early indicators of climate-driven range shifts (Fogarty *et al.* 2017) and these observations are a valuable source of information for prioritising scientific research.

1.5 – Thesis outline and objectives

This thesis encompasses four data chapters:

1. Chapter Two develops an oceanographic habitat suitability model for kingfish from eastern Australia using citizen science data and remotely-sensed environmental covariates. The objective of this chapter was to demonstrate the utility of a marine-based habitat suitability model for quantifying historical climate-driven species redistributions while simultaneously accounting for sources of natural climate variability. This chapter demonstrates that climate-driven shifts in the core and poleward edge of suitable kingfish oceanographic habitat from south-eastern Australia have already occurred, and provides the first quantitative support for anecdotal evidence of a kingfish range extension in this region.

2. Chapter Three utilises the habitat suitability model developed in Chapter Two in conjunction with dynamically downscaled oceanographic projections to assess the future environmental habitat for kingfish throughout south-eastern Australia. The objective of this chapter was to quantify the temporal persistence (months per year) of suitable oceanographic habitat for kingfish within coastal bioregions. This chapter demonstrates that temporal habitat persistence is an important metric for climate change adaptation because it provides fishery-relevant information, and highlights how novel metrics relevant to climate adaptation can be derived from projections of species' environmental habitats.

3. Chapter Four experimentally tests for sources of variation associated with the application of a novel bioelectrical impedance analysis (BIA) method for quantify fish body condition. The objective of this chapter was to develop a robust sampling protocol for the field-based application of BIA for assessing relationships between fish condition and environmental habitat suitability (Chapter 5). This chapter demonstrates that controlling for time since fish death, anatomic location of measurement and the temperature of fish tissue are important for obtaining accurate and comparable data. Protocol consideration are presented for the robust application of BIA to maximise the utility of this approach for opportunistically measuring body condition in fish.

4. Chapter Five moves beyond assessing relationships between species occurrence and environmental variables to consider how the physiological status of species relate to environmental habitat suitability. The objective of this chapter was to test for a relationship between oceanographic habitat suitability and the physiological status of kingfish from eastern Australia. This chapter considers body condition to be an integrated index of physiological status and uses bioelectrical impedance analysis to measure the condition of kingfish throughout eastern Australia over three years, adhering to the sampling protocol developed in Chapter Four. Chapter Five highlights that: (1) fish condition can respond sensitively to environmental variability and this response can be detected using oceanographic habitat suitability models, and (2) climate change may drive extensions in species range limits through spatial shifts in oceanographic habitat quality that allow individuals to persist beyond historical range boundaries without their body condition being compromised.

- Chapter 2 -

Rapid shifts in distribution and high-latitude persistence of oceanographic habitat revealed using citizen science data from a climate change hotspot [1]

2.1 - Abstract

The environmental effects of climate change are predicted to cause distribution shifts in many marine taxa, yet data are often difficult to collect. Quantifying and monitoring species' suitable environmental habitats is a pragmatic approach for assessing changes in species distributions but is underdeveloped for quantifying climate change induced range shifts in marine systems. Specifically, habitat predictions present opportunities for quantifying spatiotemporal distribution changes while accounting for sources of natural climate variation. Here we demonstrate the utility of a marine-based habitat model parameterised using citizen science data and remotely-sensed environmental covariates for quantifying shifts in oceanographic habitat suitability over 22-years for a coastal-pelagic fish species in a climate change hotspot. Our analyses account for the effects of natural intra- and inter-annual climate variability to reveal rapid poleward shifts in core (94.4 km decade^{-1}) and poleward edge (108.8 km decade^{-1}) oceanographic habitats. Temporal persistence of suitable oceanographic habitat at high-latitudes also increased by approximately three months over the study period. Our approach demonstrates how marine citizen science data can be used to quantify range shifts, but necessitates shifting focus from species distributions directly, to the distribution of species' environmental habitat preferences.

[1] **Chapter is published**: Champion, C., Hobday, A. J., Tracey, S. R., and Pecl, G. T. (2018). Rapid shifts in distribution and high-latitude persistence of oceanographic habitat revealed using citizen science data from a climate change hotspot. *Global Change Biology*, 24, 5440–5453.

2.2 - Introduction

Climate-driven species redistributions are occurring at approximately an order of magnitude faster in the marine environment than in terrestrial systems (Chen *et al.* 2011; Poloczanska *et al.* 2013; Sorte *et al.* 2010). These range shifts are altering the structure of ecosystems and affecting human societies that depend on them (Pecl *et al.* 2017; Vergés *et al.* 2014). The rapid and pervasive nature of climate-driven ecological change within marine systems highlights the need to identify changes to the distributions of key species to enhance our capacity for developing adaptive management strategies (Hobday *et al.* 2016b; Pecl *et al.* 2014b). However, poor spatiotemporal resolution of species occurrence records and a paucity of longitudinal surveys of species presence and abundance, which can describe range-shifts directly, commonly prevents the identification of a climate change signal from natural variability in species distributions (Hobday and Evans 2013).

Predicting the preferred environmental habitat for species of interest is an alternative, pragmatic approach for assessing the ecological effects of climate change across species lacking sufficient direct observations (Araújo *et al*. 2005). Species distribution models (SDMs) commonly facilitate this approach by relating available species occurrence records (presence-only or presence-absence data) with environmental variables to define habitat preferences and estimate species' distributions (Barbet-Massin *et al.* 2012; Elith *et al.* 2006). Marine-based applications of SDMs are increasing but remain under-developed (Brodie *et al.* 2018), particularly for understanding and predicting climate-driven species redistributions (Elith *et al.* 2010; Robinson *et al.* 2011). For example, pelagic fishes are predicted to undergo large spatial redistributions under climate change partly due to high adult mobility allowing these species to track their thermal preferences (Sunday *et al.* 2015). However, SDMs have identified high

seasonal variation in the distribution of environmental habitats for pelagic fishes (Brodie *et al.* 2015), suggesting a need to account for sources of natural climate variability when using SDMs to assess the effects of anthropogenic climate change on species distributions.

The physiological responses of species are predicted to vary in relation to environmental habitat suitability (Del Raye and Weng 2015). Concurrent reductions in reproduction, growth and feeding occur across a declining gradient of habitat suitability (Helaouët and Beaugrand 2009), ultimately affecting species' survival in areas of low quality habitat (Schmidt-Nielsen, 1990). Spatial projections from SDMs provide a useful summary of variation in environmental suitability that may be used to identify areas where species' physiological requirements are likely met, and where species' performance or survival may be compromised (Helaouët and Beaugrand 2009). Subsequently, spatial projections of habitat suitability may be used to identify locations where species are progressing through stages of climate-mediated range shifts (Bates *et al.* 2014). For example, small, non-viable or vagrant adult populations of marine fishes representing early stages of the range extension pathway are likely to be found in regions corresponding with low environmental habitat suitability (Bates *et al.* 2014; Booth *et al.* 2011).

Mapped indices of habitat suitability have previously been used to identify species core habitats (Hill *et al.* 2015), but are rarely used to identify shifts in the range boundaries of marine species (but see Robinson *et al*. 2015a). Combining spatial projections of species' probability of occurrence from SDMs with sampling effort information has recently proved useful for identifying range boundaries for terrestrial species based on minimum relative abundance values (Ashcroft *et al.* 2017). When sampling effort is unknown, independent species occurrence data may be compared with spatial projections from SDMs to define range boundaries or habitat edges in terms of a threshold probability of occurrence or a minimum

habitat suitability value (Champion *et al.* 2019b). Approaches that utilise data-driven criteria for defining range boundaries or edges of species suitable environmental habitats are necessary to improve measures of climate-driven range shifts derived from SDMs. For example, robust summary statistics derived from SDM spatial projections can form response variables for additional quantitative analyses (Hill *et al.* 2015; Hobday 2010), such as correlative mixed models, that are well-suited for quantifying rates of climate-driven species redistributions. Analyses that allow for random effects can facilitate the incorporation of temporal data dependency structures (Zuur *et al*., 2013) and subsequently account for the often strong influence of natural climate variability (Hobday and Evans 2013) to reveal underlying climate change signals in spatiotemporal species distribution patterns. Because species' responses to multiple environmental covariates are commonly used to make spatial projections (Brodie *et al.* 2015), this approach can also incorporate the effects of simultaneous climate-driven changes in multiple environmental variables that influence species' distributions.

Strong regional climate velocity, or relatively high rates of shifting isotherms (Burrows *et al.* 2011), is an important environmental indicator of locations where species' distributions are rapidly changing (Sunday *et al.* 2015). The marine environment adjacent to south-eastern Australia is a prominent climate change hotspot (Hobday and Pecl 2014), where climate-driven oceanographic changes have resulted in a 350 km poleward extension of isotherms between 1944 – 2002 (Ridgway 2007). By acting as natural laboratories and early learning locations, ocean warming hotspots such as south-eastern Australia provide opportunities to demonstrate approaches for better understanding climate-driven ecological change (Pecl *et al.* 2014b). Given time and resource limitations, it is important for research undertaken in climate change hotspots to prioritise species of key ecological and economic importance (Booth *et al.* 2011)

in order to maximise our capacity to develop effective adaptation options and management strategies (Hobday *et al.* 2016b; Miller *et al.* 2017).

The yellowtail kingfish *Seriola lalandi* (hereafter 'kingfish') is a coastal-pelagic species that extends along the southern coast of mainland Australia (Dempster and Kingsford 2003; Hobday and Campbell 2009). Kingfish are a high-value target species in eastern Australian fisheries, where the estimated annual recreational catch exceeds the average annual commercial catch (Henry and Lyle 2003; Lowry *et al*., 2016). Recently, observations of kingfish by recreational anglers in south-eastern Australia have been made approximately 200 km poleward of the previous southernmost occurrence record for this species (Stuart-Smith *et al.* 2016). These observations provide strong evidence for the detection of kingfish outside of its usual range, but low confidence in the historical range boundary for kingfish has resulted in overall low confidence of this species undergoing a range extension (Robinson *et al.* 2015a). Nevertheless, observations of fishes outside their usual distributions can be early indicators of climate-driven range shifts (Fogarty *et al.* 2017) and warrant further analysis.

The aim of this study was to use citizen science data of kingfish occurrences recorded by recreational anglers to create, and demonstrate the utility of, a marine-based SDM for quantifying climate-driven species redistributions while accounting for short- and long-term natural climate variability. In addition, we also (1) quantify climate-driven shifts in the core and poleward edge of suitable kingfish oceanographic habitat from south-eastern Australia from January 1996 to July 2017, and (2) quantify trends in the temporal persistence of suitable oceanographic habitat for kingfish at the poleward edge of its distribution.

2.3 - Methods

2.3.1 - Study extent

The spatial extent of this study encompassed the marine environment adjacent to eastern Australia (20-46°S, 144-160°E; Figure 2.1), where a single population of kingfish is known to occur across coastal and pelagic environments (Miller *et al.* 2011). The oceanography of this region is dominated by the poleward flowing East Australian Current (EAC), which is strengthening due to increased wind stress over a broad region of the South Pacific associated with climate change (Cai *et al.* 2005; Sloyan and O'Kane 2015). Subsequently, sea surface temperatures off south-eastern Australia have increased at a rate approximately four times the global average (Ridgway 2007), leading to the redistribution of diverse marine taxa (Malcolm and Scott 2017; Nimbs *et al.* 2016; Ramos *et al.* 2015; Robinson *et al.* 2015a; Sunday *et al.* 2015) and altered ecosystem structure (Ling 2008; Vergés *et al.* 2014) and function (Marzloff *et al.* 2016).

2.3.2 - Kingfish occurrence records

Kingfish location data (GPS coordinates) from eastern Australia were obtained from fish tagged by recreational anglers as part of a catch-and-release tagging program administered by the New South Wales Department of Primary Industries. Kingfish occurrence records had a temporal range from 1974 – present, but were restricted to 1996 – 2015 to match the availability of satellite-derived environmental covariates. Spatial and temporal independence among kingfish occurrence records was satisfied following the methods of Brodie *et al.* (2015); which involved retaining only occurrences from a unique day and location, and retaining only

those that were greater than 0.1 degree (~ 20 km) apart. Following these procedures, a total of 1,203 kingfish occurrence records were available for model fitting and cross-validation.

In order to characterise unsuitable oceanographic habitat for kingfish and provide a binomial response variable for statistical modelling, pseudo-absence points were generated inshore of the continental shelf break within the study region and randomly matched with a date from the set of occurrence records. A large number (i.e. > 10,000) of randomly selected pseudo-absences is recommended for regression-type analyses for species distributions (Barbet-Massin *et al.* 2012). Given the broad spatial scale of this study, a total of 20,000 randomly generated pseudo-absence points were selected in order to adequately describe the spatiotemporal variation in oceanographic covariates throughout the study extent (Brodie *et al.* 2015). We note that although data used to parameterise habitat models fall inshore of the continental shelf break, habitat projections are extended to the entire study area as kingfish are also known to occur in offshore pelagic environments (Gillanders *et al.* 2001).

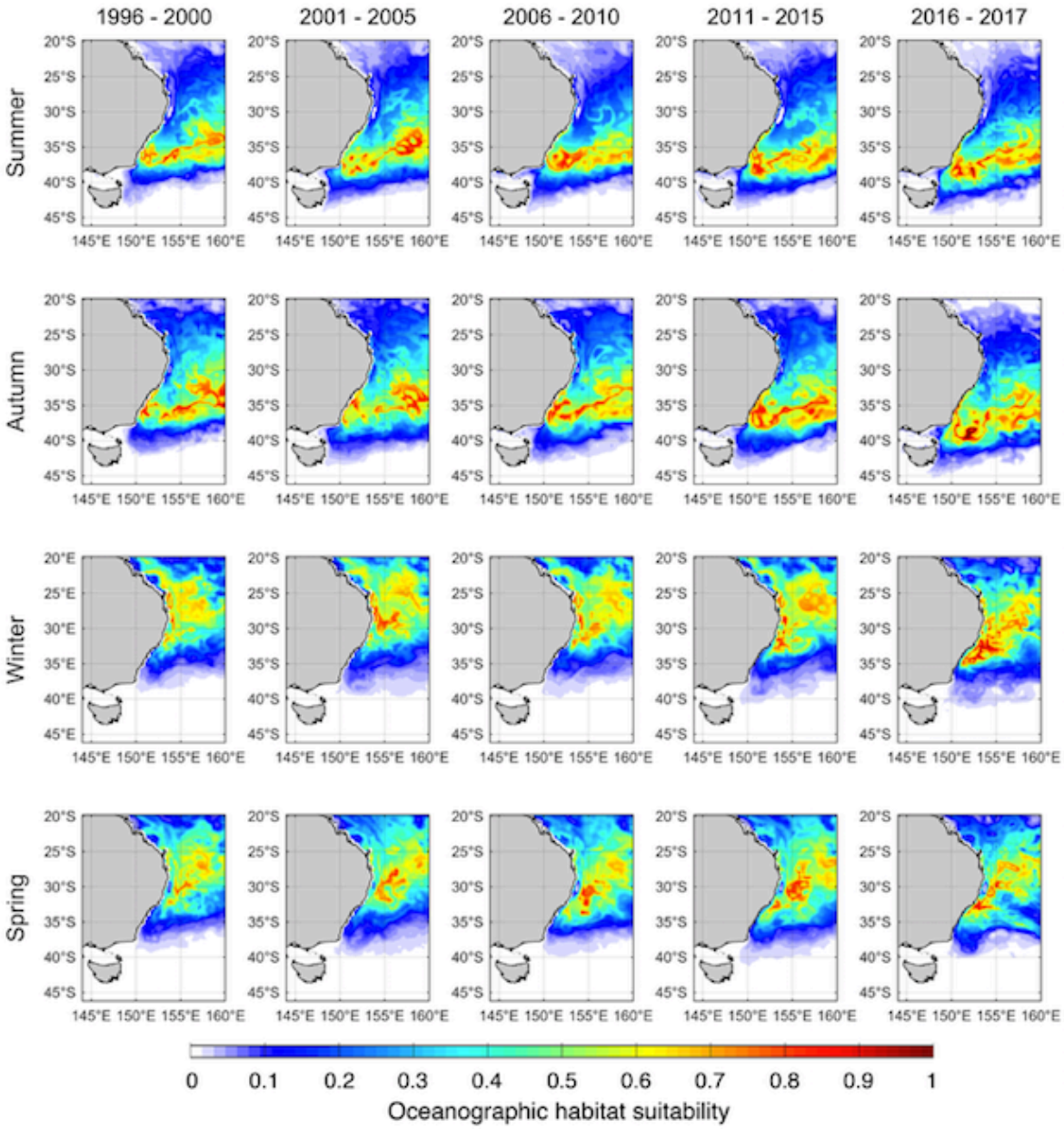

Figure 2.1. Spatial projections of kingfish oceanographic habitat suitability for eastern Australia from January 1996 to July 2017. Monthly spatial projections have been time-binned (5 years) and seasonally aggregated (Summer = December to February, Autumn = March to May, Winter = June to August, Spring = September to November). Note the most recent period covers 2016 and 2017 only.

2.3.3 - Oceanographic predictors

Explanatory oceanographic variables were initially selected based on their likely importance to coastal-pelagic fishes (Hobday and Hartog 2014) and matched to occurrence and pseudo-absence points using the Spatial Dynamics Ocean Data Explorer (Hartog & Hobday, 2011). The oceanographic variables considered for model selection were: (1) sea surface temperature (SST), (2) sea level anomaly (SLA), (3) dissolved oxygen (DO) and (4) eddy kinetic energy (EKE; Table 2.1). In this region, satellite-based chlorophyll estimates are significantly correlated with SST and have incomplete spatial and temporal coverage so were not included in model selection.

Table 2.1. Descriptions of explanatory covariates and their range of values for kingfish presence (*P*) and pseudo-absence (*pA*) points. Oceanographic predicators were interpolated to the largest common resolution (0.1°) when making spatial projections. *Explored but not included in model fitting.

Predictor	Description	Range	Units
SST	Sea surface temperature from Advanced Very High Resolution Radiometer (AVHRR) with 0.04° spatial resolution	*P*: 13 - 27 *pA*: 9 - 29	°C
SLA	Sea level anomaly from synthetic temperature and salinity (synTS; Ridgway & Dunn, 2010) with 0.1° spatial resolution	*P*: -0.2 - 0.25 *pA*: -0.3 - 0.4	m
DO*	Dissolved oxygen from CSIRO Atlas of Regional Seas (Condie and Dunn 2006) climatology with 0.2° spatial resolution	*P*: 4.5 - 6 *pA*: 3.8 - 7.5	ppm
EKE	Eddy kinetic energy derived from altimetry with 0.1° spatial resolution	*P*: 0 - 0.4 *pA*: 0 – 1.2	$m^2\ s^{-2}$
Year	Calendar year (incorporated as a random term in mixed models)	1996 - 2015	

Collinearity among predictor variables was assessed using pair plots and Spearman rank correlation coefficients. Correlated (> 0.5 and < -0.5) environmental pairs were identified and the explanatory variable with the clearest ecological interpretation from covarying pairs was retained for model selection (Zuur *et al*. 2013). A strong correlation between sea surface

temperature and dissolved oxygen (r = -0.77) resulted in the removal of dissolved oxygen from the set of oceanographic predictors prior to model selection. Because correlation coefficients only describe pairwise correlations, variance inflation factors (VIFs) were used to assess the extent of any collinearity among the remaining explanatory variables. VIFs were low (i.e. < 1.5) for all remaining explanatory variables, indicating that collinearity would not affect model performance (Zuur *et al*. 2007).

2.3.4 - Oceanographic habitat modelling

Oceanographic habitat suitability for kingfish from eastern Australia was described by applying a generalised additive mixed model (GAMM). This model used the logistic link function to relate the binomially distributed response variable (i.e. occurrence or pseudo-absence) to oceanographic predictor variables (Zuur *et al*. 2009). Calendar year was included as a proxy for fishing effort because effort information was not available in the catch-and-release database. To optimise smoothing functions and avoid over-fitting to the data, penalized regression spline type smoothers of moderate rank were applied using generalised cross validation. However, these were removed from individual predictors if their estimated degrees of freedom was approximately equal to 1, which indicates linearity with the log-of-odds transformed response variable (Zuur *et al*. 2009). The optimal GAMM has the form (in script notation):

$$Response = s(SST) + SLA + s(EKE) + (1|Year) \quad (1)$$

where *Response* is the relative probability of kingfish presence modelled as a function of sea surface temperature (*SST*), sea level anomaly (*SLA*) and eddy kinetic energy (*EKE*), with *Year*

included as a random factor. Smoothers are denoted by *s*. Furthermore, the model's *Response* was converted to an index of kingfish 'oceanographic habitat suitability' because: (1) relative probability of presence values are dependent on the ratio of occurrence to pseudo-absence data used to fit the model (Pearce and Boyce 2006), and (2) the *Response* is a function of oceanographic covariates that reflect habitat suitability and not the distribution of kingfish directly. Oceanographic habitat suitability was scaled between 0 (unsuitable) and 1 (highly suitable) by dividing all relative probability of occurrence predictions by the maximum relative probability predicted throughout the spatial and temporal extent of the study.

Forward model selection was applied using an information theoretic approach to identify single term additions from the available environmental predictors that most improved model quality (Warren and Seifert 2011). The resulting set of exploratory models contained nested covariate combinations of increasing complexity (Table 2.2), and the model in this set with the lowest Akaike information criterion (AIC) value was considered the most parsimonious model. All available occurrence data across the spatial and temporal extent of this study were used in modelling fitting.

Table 2.2. Summary of the full model and nested alternatives assessed using an AIC informed model selection procedure on covariate combinations of increasing complexity. Smoothing factors are indicated by '*s*'. Delta-AIC values denote differences in AICs between models relative to the most parsimonious model (bolded).

Iteration	Model	Variable added	ΔAIC	Mean AUC (± SD)	Mean TSS (± SD)
0	*s(SST) + (1|Year)*	-	194.432	0.713 ± 0.004	0.584 ± 0.015
1	*s(SST) + s(EKE)+ (1|Year)*	EKE	1.903	0.792 ± 0.003	0.602 ± 0.014
2	*s(SST) + s(SLA) + s(EKE)+ (1|Year)*	SLA	1.807	0.843 ± 0.003	0.611 ± 0.014
3	***s(SST) + SLA + s(EKE)+ (1|Year)***	*Smoother removed from SLA	0	0.887 ± 0.002	0.645 ± 0.013

Spatial and temporal autocorrelation was a concern in the present study because occurrence data were recorded by recreational anglers whose fishing effort may be spatiotemporally biased (e.g. favour fishing locations or fish more on weekends/holidays etc.). Autocorrelation was evaluated using spatial and temporal variograms to relate the semi-variance of points to the spatial (degrees) and temporal (days) distance separating them (Zuur *et al*. 2009, 2013). Cut-off distances were chosen to reflect the spatial and temporal limits that autocorrelation is likely to arise from angler bias, and these distances defined the limits of our assessment for autocorrelation. Dates of fish captures were converted to Julian days in order to create a temporal semi-variogram with a cut-off distance of five days. Coordinates of fish captures were used to create a spatial semi-variogram with a cut-off distance of one degree (~111 km). In exploratory analyses, both spatial and temporal correlation was judged to be consistent across distances (Figure 2.2), except at fine spatial scales (0.1 – 0.3 degrees) where there was lower correlation (higher semi-variance) than at other distances (e.g. as seen in Smith *et al*. 2017). This is likely to reflect the spatial influence of pseudo-absences existing close to occurrence observations (i.e. between 0.1 – 0.2 degrees), resulting in increased residual variation at fine

spatial scales where a binary response characterises relatively similar environmental habitats. Regardless, there was no evidence to suggest positive spatial or temporal autocorrelation in the present study, indicating that the methods for establishing independence among angler-recorded species occurrences from Brodie *et al.* (2015) were also effective in this study.

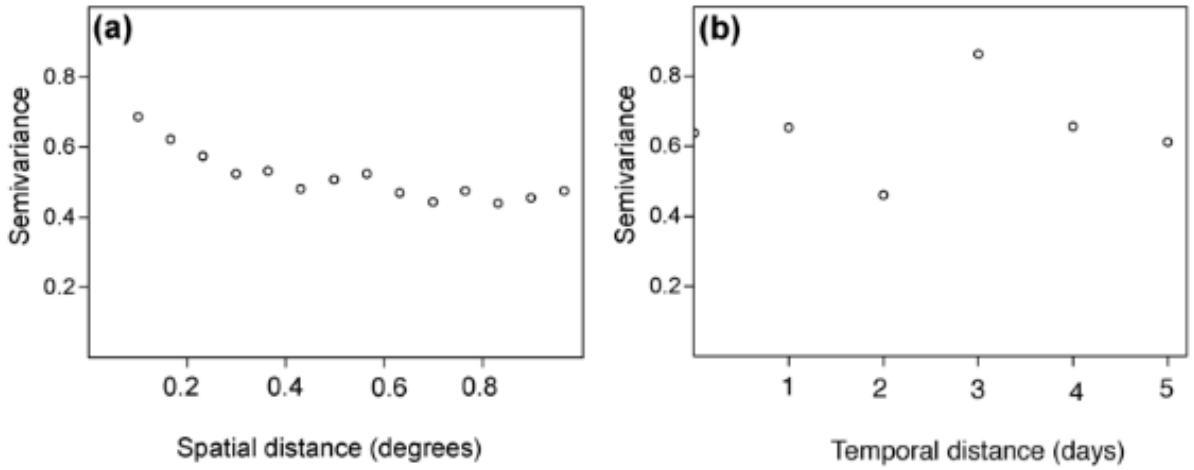

Figure 2.2. (a) Spatial and (b) temporal variograms showing the correlation of kingfish presence points with respect to the spatial and temporal distances that separate them. A straight line shows spatial independence and autocorrelation is indicated by a positive slope, usually at small *x*-values.

The accuracy and predictive skill of the optimal model was evaluated using *k*-fold cross-validation. This was done by randomly partitioning the full dataset into five subsets ($k = 5$) containing an equal number of occurrence data and a random selection of 10,000 pseudo-absences (Barbet-Massin *et al.* 2012). To compute a set of confusion matrices for calculating measures of model accuracy (Swets 1988), the optimal model was trained on each of the four subsets and each model tested against the 5th subset. Five-fold cross-validation was selected due to concern that too few occurrence data would be used to create the evaluation models if data were partitioned into a greater number of folds (Smith *et al.* 2017). The area under the receiver operating characteristic curve (AUC) and true skill statistic (TSS) are appropriate

measures of model accuracy for projections of species presence and absence in geographic space (Allouche *et al.* 2006), and are commonly used in combination when evaluating overall model skill (Brodie *et al.* 2015). Rates of true positive (sensitivity) and false positive (1-specificity) projections were used to calculate the mean AUC value from *k*-fold cross-validations. The AUC avoids the need to assume an arbitrary cut-off probability to differentiate between projections of suitable and unsuitable oceanographic habitat, and is thus a valuable measure of the accuracy of species distribution models (Elith *et al.* 2006). AUC values range from 0 – 1, where an AUC of 0.5 indicates the projection is no better than random and an AUC greater than 0.8 indicates good model accuracy (Araújo *et al.* 2005; Swets 1988). Additionally, the mean TSS was calculated as an alternative, threshold dependent, measure of model accuracy obtained from average measures of model sensitivity and specificity (i.e. TSS = sensitivity + specificity – 1). TSS values ranges from -1 to 1, where 0 or less reflects models with no predictive skill.

The optimal model was used to create monthly spatial projections of oceanographic habitat suitability for kingfish in eastern Australia from January 1996 – July 2017. This temporal range (i.e. > 20 years) is sufficient to capture long-term climate change responses (Brown *et al.* 2016) in addition to short-term seasonal and multi-year variation, and is commonly used as a minimum temporal criteria for syntheses of climate change impacts (Poloczanska *et al.* 2013; Rosenzweig *et al.* 2008). Spatial surfaces for each environmental predictor in the optimal model were interpolated to the largest common resolution (Table 2.1), and as a result all projections of kingfish oceanographic habitat were resolved to 0.1°.

2.3.5 - Range shift models

Monthly spatial projections were used to assess evidence for a latitudinal shift in the 'core' and 'poleward edge' of oceanographic habitat for kingfish from eastern Australia. Core oceanographic habitat was specified as the location of maximum oceanographic suitability in each monthly spatial projection (Robinson *et al.* 2015b). The poleward edge of suitable oceanographic habitat was determined by comparing the locations of an independent set of kingfish occurrence records, not used in model fitting, with spatial projections of modelled habitat. To do so, we compared kingfish occurrences (n = 31) recorded by the Range Extension Database and Mapping Project (Redmap; www.redmap.org.au) between March 2002 and April 2017 with day-specific projections of oceanographic habitat suitability at corresponding locations (Figure 2.3). Redmap data are particularly well-suited for identifying a minimum habitat suitability value that is likely to reflect species' range edge habitats because these observations represent species outside their usual distributions and are useful indicators of the early stages of climate-driven range shifts (Fogarty *et al.* 2017). A total of 31 day-specific projections of the poleward edge of suitable oceanographic habitat were created with 0.1° spatial resolution, and oceanographic suitability values for grid cells containing Redmap occurrence records were extracted from each of these projections (Figure 2.3). The minimum habitat suitability value (min = 0.064) from the resulting dataset was considered to represent the edge of suitable oceanographic habitat for kingfish in this study. This is likely to be a conservative estimate for the edge of suitable oceanographic habitat for kingfish given the minimum value has been determined using only 31 observational data points. Regardless, our objective was to quantify relative change in the distribution and temporal persistence of kingfish habitat, which is possible if the criteria used to define the core and poleward edge of suitable habitats are held constant throughout the study period.

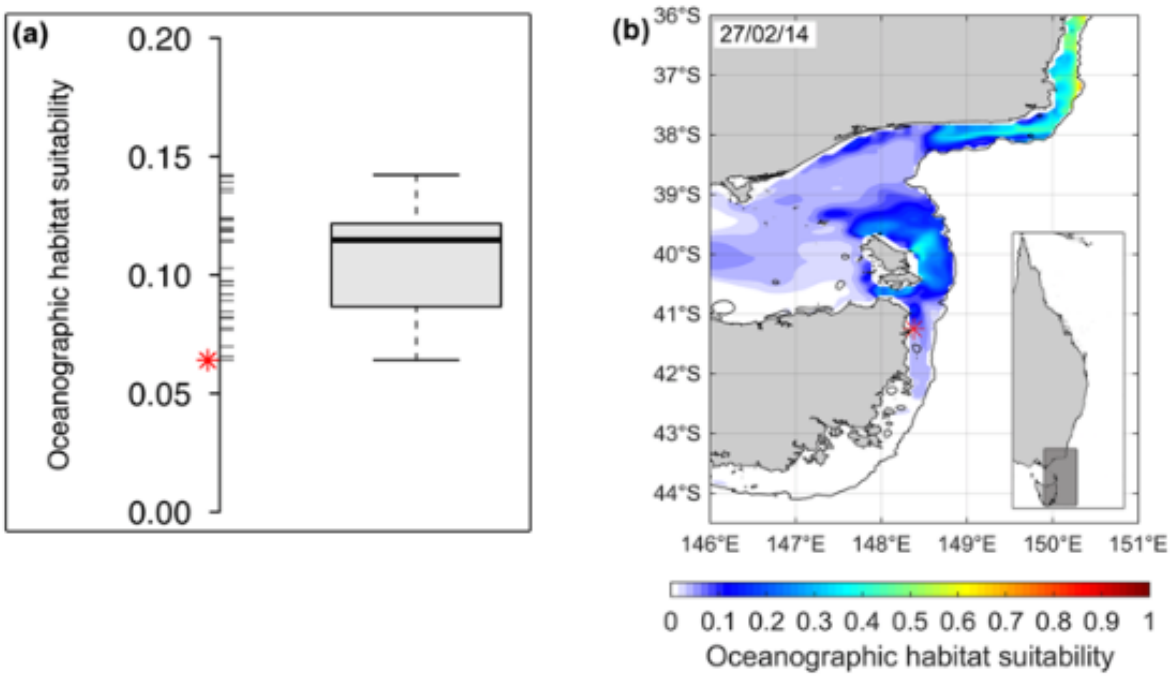

Figure 2.3. (a) Distribution of oceanographic suitability values corresponding with Redmap occurrence records (n = 31) derived from day-specific habitat projections. The minimum value from this distribution (min = 0.064) was chosen to represent the poleward edge of kingfish oceanographic habitat. (b) Example of a day-specific kingfish habitat projection matched with Redmap occurrence record (red asterisk) used to create the distribution in (b).

Climate-driven shifts in the core and poleward edge of oceanographic habitat were assessed using linear mixed effects models to test for latitudinal trends in suitable oceanographic habitat through time, while accounting for natural climate variability. Initially, simple linear models testing for latitudinal trends in kingfish habitat through time were applied and residuals plotted against sources of natural intra- and inter-annual climate variability to assess for dependence between observations from the same month (intra-annual variability) and El Niño Southern Oscillation (ENSO; inter-annual variability) state (Southern Oscillation Index). There was evidence that the spatial distribution of kingfish oceanographic habitat was dependent on 'month' and 'ENSO state' (Figure 2.4). Subsequently, dependency structures among spatial projections of core and poleward edge habitats from the same 'month' and 'ENSO state' were incorporated in linear mixed models (Zuur *et al.* 2013). This was done so that spatiotemporal

shifts in oceanographic habitat would be estimated through time while accounting for sources of natural climate variability. The resulting linear mixed effects model has the form (in script notation):

$$Response = Year + (1|Month) + (1|ENSO\ state) \quad (2)$$

where *Response* is the latitudinal value corresponding to the location of core and range edge oceanographic habitats for kingfish (separate models for core and range edge habitats) modelled as a function of time (*Year*), with *Month* and *ENSO state* included as random terms. Rates of spatial shifts (km decade^{-1}) were derived from models fitted to monthly latitudinal projections of core and poleward range edge habitats from January 1996 to July 2017 because continuous time series more accuracy quantify rates of change than infrequent measures (Brown *et al.* 2016).

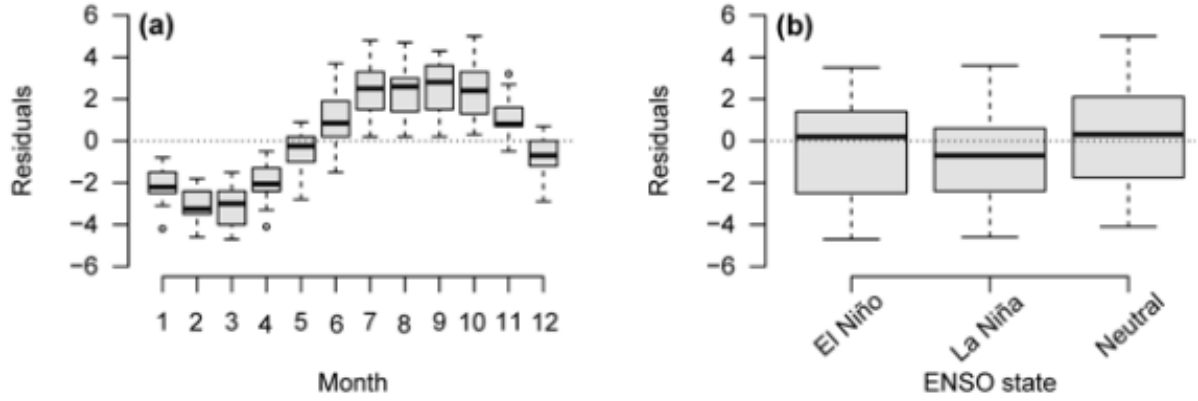

Figure 2.4. Residuals from a simple linear model for the poleward latitudinal extent of core oceanographic habitat for kingfish as a function of time (year) plotted against factors that describe natural intra- (month) and inter-annual (ENSO state) climate variability. Patterns evident in residuals across months and ENSO states are accounted for through the inclusion of these factors as random effects in linear mixed effects models (Zuur *et al*. 2013).

Finally, the temporal persistence of suitable oceanographic habitat in novel, high-latitude areas was calculated as the number of months per year that the poleward edge of suitable oceanographic habitat (as defined herein) occurred south of 41°S (i.e. within Tasmanian waters; Stuart-Smith *et al*. 2016). Simple linear models were used to test for trends in temporal persistence (months per year) from 1996 – 2016. Residual plots were assessed visually to confirm both simple linear and linear mixed effects models satisfied assumptions of normality and homogeneity of variance.

Statistical analyses were undertaken using the R programming language (R Core Team 2017): GAMMs were fitted using the 'gamm4' package (Wood and Scheipl 2016), spatial and temporal semi-variograms were constructed using the 'gstat' package (Gräler *et al*. 2016), *k*-fold cross validation was undertaken using the 'dismo' package (Hijmans *et al*. 2013) and linear mixed effects models were fitted using the 'lme4' package (Bates *et al*. 2014).

2.4 - Results

2.4.1 - Oceanographic habitat model

Spatial projections of oceanographic habitat from January 1996 – July 2017 show seasonal variation in the distribution of suitable kingfish habitat in eastern Australia, which undergoes an annual poleward extension during the Austral summer and autumn and retreats to lower latitudes during winter and spring (Figure 2.1).

The optimal model for kingfish oceanographic habitat contained the predictors sea surface temperature, sea level anomaly and eddy kinetic energy (Table 2.2), demonstrating that the

distribution of kingfish from eastern Australia is driven by simultaneous responses to multiple oceanographic factors. SST and EKE were highly significant, nonlinear, predictors of kingfish habitat suitability (Table 2.3; Figure 2.5a and 2.5c). SST had a clear, unimodal influence on habitat suitability, with the maximum positive effect on model parameters occurring at approximately 22°C (Figure 2.5a). The effect of EKE on habitat suitability was more complex, but generally had a positive effect on model parameters then declined at values greater than approximately 0.11 $m^2 s^{-2}$ (Figure 2.5c). The smoothing function was dropped from SLA in the optimal model in favour of a positive linear term (Figure 2.5b), which was a marginally significant predictor of habitat suitability (Table 2.3).

Table 2.3. Summary of results for the optimal kingfish habitat suitability model. Smoothing factors are denoted by *s*.

Variable	Effective degrees of freedom	Coefficient estimate	*P*-value
s(SST)	5.01	- 0.25	< 0.001
SLA	-	1.21	0.04
s(EKE)	7.78	2.28	< 0.001
$Year_{(intercept)}$	-	- 5.55	< 0.001

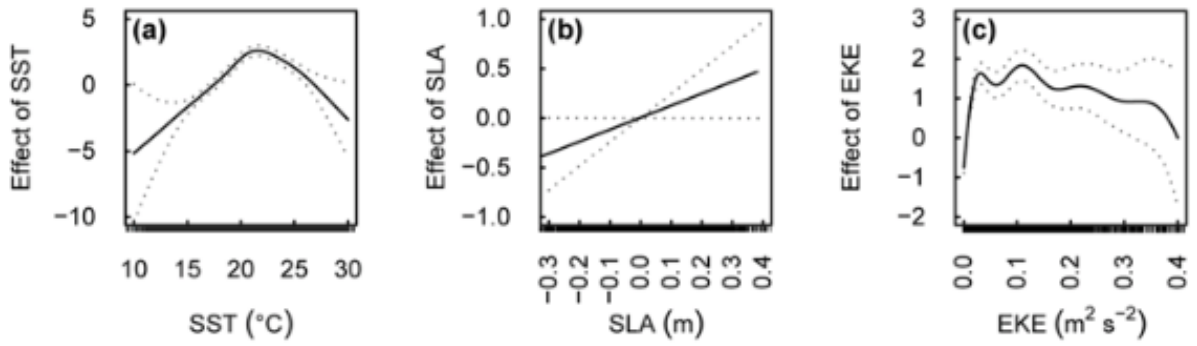

Figure 2.5. Partial effects of (a) sea surface temperature (SST), (b) sea level anomaly (SLA) and (c) eddy kinetic energy (EKE) on the fitted values of the optimal kingfish habitat model, bound by 95 % confidence intervals (dashed lines). Rugs on the *x*-axes indicate presence and pseudo-absence data for each predictor.

Five-fold cross validation revealed that the optimal model had good predictive accuracy (mean AUC = 0.887 ± 0.002 SD) according to the AUC interpretation criteria of Swets (1988), and that predictive skill (mean TSS = 0.645 ± 0.013 SD) exceeded the acceptable standard for conservation planning applications (Pearce and Ferrier 2000). Mean values of the TSS and AUC statistics indicate that the optimal model contained an appropriate number and combination of environmental predictors to effectively describe suitable oceanographic habitat for kingfish from eastern Australia and provided reliable spatial projections for subsequent range shift analyses.

2.4.2 - Range shift analyses

Linear mixed effects models revealed significant poleward shifts in the core and poleward edge of oceanographic habitat for kingfish from eastern Australia (Figure 2.6). Core oceanographic habitat was found to have shifted towards higher latitudes at a rate of 94.4 km decade^{-1} from 1996 – 2017 (50.5 - 137.9 km decade^{-1} 95 % CI; Figure 2.6a; parameters for fixed component of the model: int = 136.91, slope = -0.09, t = 4.20, P < 0.0001; intra-class correlation coefficients for random terms: month = 0.72, ENSO state = 0.02). The random 'ENSO state' term was dropped from the model predicting latitudinal values for core oceanographic habitat due to having a negligibly low intra-class correlation coefficient. This indicates that the spatial distribution of core oceanographic habitat for kingfish from eastern Australia was not dependent on ENSO state over the temporal extent of this study. The poleward edge of suitable oceanographic habitat for kingfish was also found to have shifted towards higher latitudes from 1996 – 2017 at a rate of 108.8 km decade^{-1} (87.1 – 128.2 km decade^{-1} 95 % CI; Figure 2.6b; parameters for fixed component of the model: int = 153.72,

slope = -0.09, t = 9.55, P < 0.0001; intra-class correlation coefficients for random terms: month = 0.86, ENSO state = 0.14).

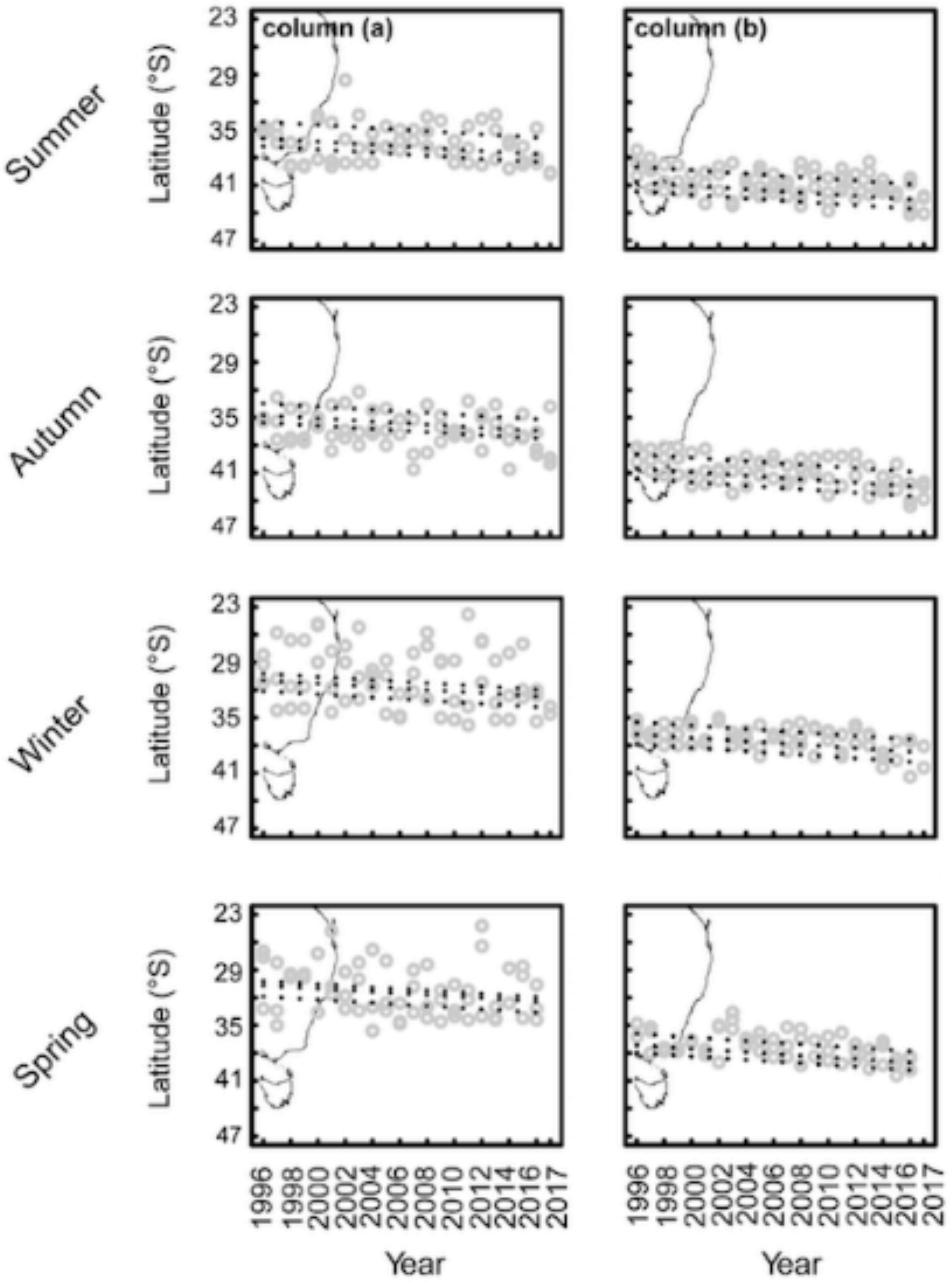

Figure 2.6. Seasonally explicit latitudinal trends in monthly projections of the (a) core and (b) poleward edge of suitable oceanographic habitat for kingfish. Dashed lines represent monthly trends fitted as a random effect within linear mixed effects models. The Australian coastline has been underlaid to aid spatial interpretation of the trends presented.

The temporal persistence of the poleward edge of suitable oceanographic habitat for kingfish poleward of 41°S was found to have significantly increased from 1996 to 2017 (Figure 2.7). Specifically, the number of months per year that oceanographic habitat suitable for kingfish occurred poleward of 41°S increased from ~ 2 months in 1996 to ~ 5 months in 2016 (Figure 2.7; int = -318.41, slope = 0.19, $F_{1, 19} = 36.92$, $P < 0.001$).

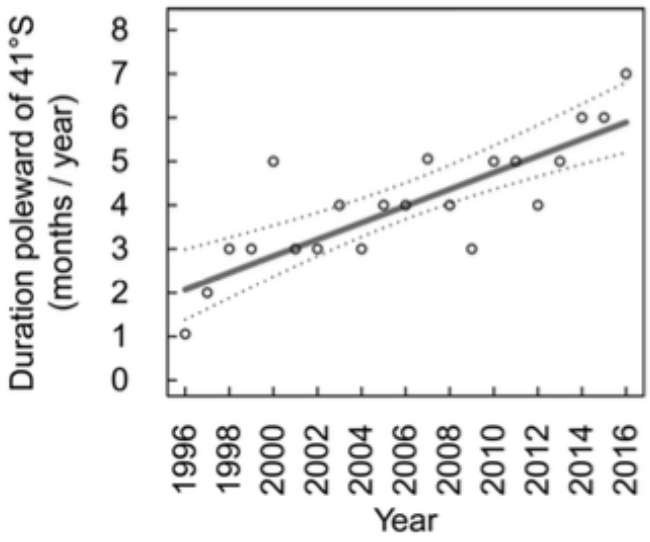

Figure 2.7. Temporal persistence of the poleward edge of suitable kingfish oceanographic habitat south of 41°S (i.e. the northern edge of the Tasmanian coastline; $r^2 = 0.68$). Dashed lines denote the 95 % confidence interval.

2.5 - Discussion

Given that spatial shifts in large numbers of marine species are expected with climate warming (Poloczanska *et al.* 2013; Sunday *et al.* 2012), pragmatic approaches that utilise increasingly available marine-based citizen science data sources (Bonney *et al.* 2014; Dickinson *et al.* 2012; Pecl *et al.* 2014a) to quantify species redistributions are required (Hill *et al.* 2015). Here, we demonstrate the utility of a marine habitat suitability model fitted using

citizen science data for quantifying climate-driven spatiotemporal shifts in oceanographic habitat, while accounting for the effects of natural intra- and inter-annual climate variability.

Our approach revealed that core oceanographic habitat for kingfish from south-eastern Australia has shifted poleward at a rate of 94.4 km decade^{-1} in response to climate-driven changes in regional oceanography, while the leading edge of suitable habitat was found to be extending poleward at a rate of 108.8 km decade^{-1}. The velocity of this poleward distribution shift is notably faster than historical rates of range change identified for a suite of nearshore fishes using observational data (average rate of range change = 38 km decade^{-1}; Sunday *et al*., 2015) and for a mobile apex predator using habitat suitability projections (88.2 km decade^{-1}; Hill *et al*., 2015) from eastern Australia. Our results also markedly exceed future rates of poleward range shifts predicated for 16 commercially important offshore pelagic species from Australia by the year 2100 (average rate of range change = 40 km decade^{-1}; Hobday 2010), suggesting the contemporary effects of climate change may be driving the redistribution of coastal-pelagic marine fishes faster than nearshore or truly pelagic species. Importantly, our results are based on projections of oceanographic habitat suitability determined from kingfish occurrences, which are known to produced faster range shift estimates than abundance-based measures that better reflect whole populations (Brown *et al.* 2016).

The velocity of spatial shifts in kingfish oceanographic habitat was found to be greater for the poleward range edge than for the core habitat. Spatial variation in the velocity of shifts across the distribution of suitable environmental habitat for marine species is likely to be closely linked with the effects of climate change on regional oceanography. Increased wind stress over a broad region of the South Pacific associated with climate change has resulted in a poleward advance of the south-flowing EAC (Cai *et al.* 2005; Sloyan and O'Kane 2015). Subsequently,

sea surface temperature off Tasmania (i.e. the region corresponding to the poleward edge of oceanographic habitat herein) has risen at a rate of 2.28°C century^{-1} (Ridgway 2007). Because the effect of temperature on species occurrence is commonly non-linear (Elith and Leathwick 2009), usually displaying a unimodal peak representative of species' thermal optima (Arrizabalaga *et al.* 2015; Brodie *et al.* 2017; Lien *et al.* 2014), the effects of ocean warming on species habitat suitability are similarly non-linear. For this reason, marked increases in habitat suitability for temperate marine ectotherms are likely in high-latitude environments due to ocean warming, whereas similar levels of warming in environments that already represent species' thermal preferences, such as core habitats, will have a relatively smaller effect on habitat suitably. For example, a greater positive effect of SST on kingfish habitat suitability (i.e. increase in y-axis value in Figure 2.5a) will result from a 1°C increase in cooler environments (e.g. 16°C) as opposed to the same level of ocean warming in thermally optimum habitats (e.g. 22°C). These findings, viewed in light of recent increases in sea surface temperature off south-eastern Australia, explain the strong velocity of the poleward shift in kingfish range edge habitat from this region and also account for variation between rates of range change identified for core and range edge oceanographic habitats.

Intra-annual variation in the distribution of suitable environmental habitats for coastal-pelagic species (Brodie *et al.* 2015) is likely to underpin climate-driven range shifts over decadal time-scales. Oceanographic habitat for kingfish off eastern Australia was found to extend poleward during the austral summer/autumn and retreat to lower latitudes during winter/spring. However, the effects of climate change on intra-annual spatiotemporal trends such as these are often overlooked when quantifying species redistributions, particularly for marine species that associate with dynamic oceanographic features (Mannocci *et al.* 2017). In coastal and pelagic systems, temporal persistence of suitable environmental habitat is an important factor that can

both facilitate and restrict species movements (Briscoe *et al.* 2016). Similarly, the duration of suitable habitat within novel environments is a critical factor for predicting the ecological effects of range-shifting species (Champion *et al.* 2019b). For example, ocean warming has increased the proportion of winter months that exceed the thermal threshold for larval development of the poleward extending long-spine urchin *Centrostephanus rodgersii* at their range edge in Tasmania (Ling *et al.* 2009), contributing to increased grazing pressure on macroalgal beds (Ling and Johnson 2009).

Creating monthly spatial projections of oceanographic habitat over a 22-year period allowed for intra-annual temporal trends in the distribution of suitable habitat to be investigated. It was previously believed the southern range boundary for kingfish from Australia was located at approximately 41.5°S (Atlas of Living Australia, 2016), but recent photo-verified observations of kingfish from approximately 43.5°S have been reported (Stuart-Smith *et al.* 2016). Subsequently, our analysis focused on the number of months per year that the poleward edge of suitable oceanographic habitat persisted poleward of 41°S, and revealed that a significant increase has occurred between 1996 to 2016. These findings add considerable detail to species redistribution analyses that can be used to infer a level of confidence in range shifts. Bates *et al.* (2014) propose that range extensions occur as a sequence of arrival, population increase, and persistence, and that confidence in species range changes also increases as colonisation progresses across this spectrum. Increased persistence of suitable environmental habitat at species range edges, as for kingfish, indicates greater opportunity for individuals to progress through critical life history stages, allowing for population increases and ultimately persistence in novel environments (Ling *et al.* 2009).

Intra-annual shifts in the persistence of suitable oceanographic habitat are also relevant to range-shifting species targeted in commercial and recreational fisheries. For example, greater fishing opportunity for kingfish off Tasmania is likely to result from the increasing number of months per year that suitable oceanographic conditions for this species is persisting at higher-latitudes. Assessing the effects of climate change on the temporal persistence of suitable habitat in the spatial domains of different commercial and recreational fisheries is an appropriate avenue for the development of spatially explicit adaption strategies (Champion *et al.* 2019b; Eveson *et al.* 2015), and one that requires further work (e.g. Chapter 3 of this thesis).

Like other studies of distribution shifts in pelagic fishes (Dell *et al.* 2011; Hill *et al.* 2015; Hobday 2010; Robinson *et al.* 2015b), our results are derived from spatial projections of oceanographic suitability and thus do not directly represent spatiotemporal changes in kingfish distribution. Instead, our results reflect climate-driven shifts in the combination of environmental variables that define suitable oceanographic habitat for this species. Inferring changes in species distributions from spatial shifts in their environmental habitat preferences reflects the limitations of marine citizen science data sources for quantifying species distributions. For example, the utility of presence-only citizen science data for quantifying species distributions is affected by sample size (Stockwell and Peterson 2002) and spatiotemporal sampling biases (Phillips *et al.* 2009; Stolar and Nielsen 2015), which are particularly relevant to marine applications due to the relative difficulty of accessing and observing marine habitats (Dickinson *et al.* 2010; Hobday and Evans 2013). While our study had the luxury of a large marine citizen science dataset (i.e. > 1000 occurrence records), this is unlikely to be the case for all citizen science programs where low sample size combined with sampling biases may compromise robust SDM application. Nevertheless, marine citizen science programs are becoming increasing valuable for characterising species habitat

preferences as more data are reported (Pecl *et al.* 2014a) and biases are addressed by recording observational effort (Edgar and Stuart-Smith 2014) or data removal procedures (Brodie *et al.* 2015). Range shift analyses for marine species based on projections of environmental suitability, like those herein, capitalise on citizen science data for understanding species redistributions, but also limit the interpretation of results to species' preferred environmental habitats and not their distributions directly.

Quantifying shifts in species range boundaries is an important priority for species redistribution science (Bonebrake *et al.* 2017), yet difficulty identifying ranges edges from observational data make distinguishing shifts problematic (Ashcroft *et al.* 2017). For example, range boundaries determined directly from occurrence data are sensitive to sampling intensity (Brown *et al.* 2016), and variation in sampling effort through time can lead to incorrectly inferring range edge shifts (Bates *et al.* 2015; Hassall and Thompson 2010). Instead, studies have focused on the mean or centroid location of species occurrence records (Maclean *et al.* 2008; Shoo *et al.* 2006), which allow for changes in species core habitat to be assessed, but neglect range edges. Spatial projections from SDMs with proven predictive skill provide an opportunity to define clear criteria for the extended range boundary, for example, in terms of a minimum relative abundance threshold derived from SDM projections and sampling effort information (Ashcroft *et al.* 2017). Methods to select habitat edge thresholds will likely vary for species with differing traits. For example, marine species with high adult mobility, such as kingfish, generally occupy broad latitudinal ranges (Sunday *et al.* 2015), and periodically encounter areas of low environmental habitat suitability at their range edges due to dynamic oceanographic processes (Briscoe *et al.* 2016). Therefore, it is pragmatic and conservative to match independent observational data from species putative range edges with spatial projections from SDMs to determine threshold values that maximise the agreement between observed and predicted

distributions and the interpretability of results (Liu *et al.* 2005). This approach for determining habitat suitability thresholds is dependent on the response of single individuals and our ability to detect them (Brown *et al.* 2016), and spatial shifts in threshold habitats are likely to represent a relatively small number individuals from a population expanding into new environments (Booth *et al.* 2011).

Sources of natural climate variability occurring at intra- and inter-annual time-scales strongly influences species distributions and abundance (Lehodey *et al.* 2006; Polovina 1996; Zanardo *et al.* 2017), and efforts to account for these are necessary to reveal the effects of contemporary climate change. Our results indicate that oceanographic habitat for kingfish from eastern Australia is subject to substantial monthly variability (Figure 2.4) in response to the intra-annual extension and contraction of the EAC (Young *et al.* 2011). While seasonal variability in pelagic fish distributions from eastern Australia have been documented (Brodie *et al.* 2015; Brodie *et al.* 2017), spatial projections of kingfish habitat at a monthly temporal resolution have not previously been made. Doing so improved our ability to account for intra-annual variation in kingfish oceanographic habitat when assessing spatial shifts over the 22-year study period. Specifically, this approach allowed for a dependency structure between observations from the same 'month', rather than 'season,' to be incorporated into our range shift models, which reduced standard error estimates and improved confidence in the rates of change reported for kingfish oceanographic habitat from eastern Australia.

This chapter also considered the influence of natural climate variability on environmental habitat for kingfish at inter-annual time-scales, and is among few examples from the marine realm that have attempted to account for these effects in order to delineate a climate change signal from natural variation (Hill *et al.* 2015). The influence of ENSO state on the distribution

of kingfish habitat in the study region was relatively minor, and only detectable at the poleward boundary of suitable oceanographic habitat. La Nina phases were associated with a slight poleward advance of range edge habitat, which concurs with effects of ENSO on the distribution of black marlin (*Istiompax indica*) from eastern Australia (Hill *et al.* 2015). Subsequently, only range shift models that assessed for distribution shifts in the poleward range boundary included 'ENSO state' as a random effect, and doing so led to a minor reduction in standard error estimates. Accounting for the short- and long-term influences of natural climate variability should be a key consideration when seeking to attribute spatiotemporal shifts in species distributions to anthropogenic climate change, and we demonstrate that correlative mixed-effects models provide a suitable quantitative framework for doing so.

While SDMs are broadly used to infer spatial responses of species to changing environmental conditions (Bonebrake *et al.* 2017), particularly in terrestrial systems (Elith *et al.* 2010), few attempts have been made to utilise their spatial output to quantitatively assess marine range-shifts while accounting for sources of natural climatic variation (Hill *et al.* 2015). Given the utility of citizen science observations for fitting marine-based SDMs, and trends of increasing access to these data sources (Kullenberg and Kasperowski 2016), we suggest this approach as a pragmatic method for assessing the effects of climate change on the distributions of species that have been poorly observed. However, we note that this approach necessitate that subsequent range shift analyses focus on spatiotemporal shifts in species' suitable environmental habitats and not their distributions directly, limiting the interpretability of results. This approach is likely to prove more informative for coastal and pelagic species that strongly associate with oceanographic variables (Hobday and Hartog 2014) and less informative for highly reef-associated species where habitat suitability is related to non-environmental predictors, such as distance to reef structure (Champion *et al.* 2015). Biotic

factors (e.g. prey availability) are also likely to have an important effect on the realised distribution and temporal persistence of kingfish (Mellin *et al.* 2016). To extend the interpretation of our results from the oceanographic habitat for kingfish to the distribution of kingfish directly would also require consideration of climate-driven effects on, for example, the spatiotemporal distribution of important prey species (Potts *et al.* 2016).

Given that poleward shifts in the distributions of marine species are expected to continue in response to climate-induced changes in regional oceanography (Poloczanska *et al.* 2012), projections of suitable environmental habitat for key species under future climate change scenarios are now required to underpin adaptation strategies (Hobday *et al.* 2011a; Hobday *et al.* 2016c). It is important that future projections of dynamic marine habitats are made over time-scales that are relevant to natural resource managers and user groups (e.g. recreational and commercial fishers). These time-scales may range from seasonal predications to assist quota-limited commercial fisheries (Eveson *et al.* 2015; Hobday *et al.* 2016c), to yearly projections (i.e. political time-scales) that aid natural resource managers in the development of climate change adaptation strategies. For example, analyses that quantify the temporal persistence of suitable habitat for species of interest over yearly periods, like those presented herein, may be used to trigger management responses (Champion *et al.* 2019b).

Recent advances in the ability to forecast more oceanographic variables under climate change scenarios (Payne *et al.* 2017) hold great potential to improve future estimates of species distributions, which have traditionally been restricted to forecasts of sea surface temperature alone (Brodie *et al.* 2017; Eveson *et al.* 2015). The inclusion of multiple environmental predicators in habitat forecasts will facilitate an improved understanding of the effects of

climate change on species distributions and increase our capacity to anticipate and respond to these changes.

- Chapter 3 -

Changing windows of opportunity: Past and future climate-driven shifts in temporal persistence of kingfish (*Seriola lalandi*) oceanographic habitat within south-eastern Australian bioregions [2]

3.1 - Abstract

Climate-driven shifts in species distributions are occurring rapidly within marine systems and are predicted to continue under climate change. To effectively adapt, marine resource users require information relevant to their activities at decision-making timescales. We model oceanographic habitat suitability for kingfish (*Seriola lalandi*) from south-eastern Australia using multiple environmental variables at monthly time steps over the period 1996 – 2040. Habitat projections were used to quantify the temporal persistence (months per year) of suitable oceanographic habitat within six coastal bioregions. A decline in temporal habitat persistence is predicted for the northernmost (equatorward) bioregion, while increases are predicted for the three southernmost (poleward) bioregions. We suggest that temporal habitat persistence is an important metric for climate change adaptation because it provides fishery-relevant information. Our methods demonstrate how novel metrics relevant to climate adaptation can be derived from projections of species' environmental habitats, and are appropriate for the management of fisheries resources and protection of high conservation value species under future climate change.

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3.2 - Introduction

Climate change is driving a global redistribution of biodiversity (Pecl *et al.* 2017), with shifts in species distributions occurring approximately an order of magnitude faster in marine environments than in terrestrial systems (Chen *et al.* 2011; Poloczanska *et al.* 2013; Sorte *et al.* 2010). The poleward direction of these shifts is consistent among diverse groups of marine taxa (Poloczanska *et al.* 2013), and symptomatic of the predicted and realised effects of climate change on oceanographic variables (Cai *et al.* 2005; Sloyan and O'Kane 2015; Sorte *et al.* 2010; Wu *et al.* 2012). The rapid and pervasive ecological effects of climate change within marine systems highlights the urgent need to undertake research focused on the development of human adaptation strategies (Hobday *et al.* 2016b; Pecl *et al.* 2014b). While qualitative assessments of species vulnerability to climate change can inform adaptation approaches (Pecl *et al.* 2014c; Robinson *et al.* 2015a), quantitative assessments tailored to assist decision making in the face of rapid global change remain relatively undeveloped. For example, quantitative analyses of species redistributions commonly focus on estimating rates of range change over decadal timescales (Hill *et al.* 2015), which can be difficult for stakeholders to interpret and do not reflect management timeframes (i.e. months to years). Analyses of past and future climate-driven ecological change that produce metrics of direct relevance to stakeholders that are calculated over shorter timescales are required to aid decision making (Hobday *et al.* 2016c). These attributes are not commonly represented among quantitative assessments of climate-driven marine species redistributions, presently limiting their utility for climate adaptation.

The temporal persistence of suitable environmental habitat, or the duration that preferred environmental conditions are sustained in particular regions, restrict and facilitate the movements of many coastal and pelagic species (Briscoe *et al.* 2016). Shifts in temporal persistence of species' environmental habitats is an important, yet underappreciated, aspect of

climate-driven species redistributions (Champion *et al.* 2018b), and one that has tangible implications for stakeholders. Specifically, the duration of environmental habitat persistence in spatially explicit domains is linked to ecological, social and economic opportunity. Ecologically, the temporal persistence of suitable habitat within novel environments is a critical factor influencing range shifting species. Bates *et al.* (2014) proposed that climate-driven range extensions occur as a sequence of arrival, population increase, and persistence, and that confidence in species range change also increases as 'colonisation' progresses across this spectrum. Therefore, increased temporal persistence of suitable environmental habitat at species range edges indicates greater opportunity for individuals to progress through critical life history stages, allowing for population increases and ultimately the establishment of species in novel environments (Ling *et al.* 2009). Socially and economically, changes in the temporal persistence of suitable habitats for valuable or iconic species may equate to shifts in commercial and recreational fishing opportunity. Similarly, the economic profitability of tourism ventures, such as charter fishing operations or SCUBA diving tours, may be affected by these changes. When communicated as a measure of opportunity, future projections of temporal habitat persistence can provide a quantitative basis for the development of climate change adaptation strategies. For example, projections of increased habitat persistence for commercially valuable species may support greater investment from fishers, such as the purchase of gear or licences, while predicted declines in habitat persistence may indicate a potential need to divest or diversify.

Defining species environmental habitat preferences and projecting these in space and time has proven useful for assessing the long-term effects of climate change on species distributions (Araújo *et al.* 2005; Elith *et al.* 2010). Species distribution models (SDMs) typically facilitate this approach by providing a framework for estimating the spatial distribution of species'

habitats as a function of environmental variables (Renner *et al.* 2015). These models, also known as habitat suitability models (Keith *et al.* 2008), are valuable quantitative tools particularly when used for dynamic ocean management (Briscoe *et al.* 2016; Hobday *et al.* 2013; Scales *et al.* 2014). For example, projections of environmental conditions and habitats for key species represent decision support tools for commercial (Eveson *et al.* 2015; Hobday *et al.* 2011b) and recreational (Brodie *et al.* 2017) fisheries and aquaculture (Hobday *et al.* 2016c; Spillman and Hobday 2014). Quantifying climate driven changes in the temporal persistence of species' environmental habitats is possible when calibrated habitat suitability models are used to make regular (e.g. monthly) spatial projections through time. In this way, estimates of species' temporal persistence (e.g. months per year) can be derived within spatially explicit domains and over management-relevant timescales. Recent advances in the ability to forecast a greater suite of oceanographic variables under climate change scenarios (Payne *et al.* 2017) will improve future estimates of species distributions and temporal persistence of environmental habitats. To date, future habitat projections have generally been restricted to forecasts of sea surface temperature alone (Brodie *et al.* 2017; Eveson *et al.* 2015), and the inclusion of multiple environmental predicators in habitat forecasts will increase our capacity to anticipate and respond to change (Kaplan *et al.* 2016).

The marine environment adjacent to south-eastern Australia is among the most rapidly warming regions of the global ocean (Hobday and Pecl 2014). The oceanography of this region is dominated by the poleward flowing East Australian Current (EAC), which is strengthening due to increased wind stress over a broad region of the South Pacific associated with climate change (Cai *et al.* 2005; Sloyan and O'Kane 2015). In response, the distributions of diverse marine taxa have been documented undergoing poleward shifts (Malcolm and Scott 2017; Nimbs *et al.* 2016; Ramos *et al.* 2015; Sunday *et al.* 2015). Such shifts have already resulted

in novel species interactions, causing observed regime changes among multiple ecosystems in the region (Ling 2008; Vergés *et al.* 2014; Wernberg *et al.* 2016).

The yellowtail kingfish *Seriola lalandi* (hereafter 'kingfish') is targeted in several eastern Australian fisheries, where the estimated annual recreational catch exceeds the average annual commercial catch (Henry and Lyle 2003, Lowry *et al*., 2016). Recent analyses have revealed that the distribution of oceanographic habitat for kingfish from eastern Australia has rapidly shifted poleward over the last 20 years (Champion *et al.* 2018b). Additionally, observations of kingfish between 2010 – 2015 by recreational anglers in south-eastern Australia have been recorded approximately 200 km poleward of the previous southernmost occurrence record for this species (Stuart-Smith *et al.* 2016). These findings suggest that the distribution of kingfish is undergoing a poleward range extension in south-eastern Australia, and it is likely that fishers and managers will need to adapt to these changes in the future.

This study utilises a habitat suitability model for kingfish from eastern Australia (developed in Chapter 2) to create past and future projections of suitable environmental habitat, using multiple oceanographic predictors. We aim to quantify climate-driven shifts in the temporal persistence of suitable kingfish oceanographic habitat in six south-eastern Australian marine bioregions for the period 1996 to 2040. Our analyses demonstrate how temporal habitat persistence can be quantified and related to climate adaptation options, which may assist other studies aiming to reduce the vulnerability of coastal communities to climate change by building the capacity of marine users to adapt.

3.3 - Methods

3.3.1 - Study region

The spatial extent of this study encompassed the marine environment adjacent to south-eastern Australian between 28 – 44°S, and was restricted to the coastal-pelagic environment nearshore of the continental shelf break where the majority of fishing for kingfish occurs. A single, genetically distinct population of kingfish is known to occur within this region (Miller *et al.* 2011) and individuals occupy both coastal and pelagic environments (Gillanders *et al.* 2001).

The study extent was divided into six marine bioregions, which include the Tweed-Morton, Manning Shelf, Hawkesbury Shelf, Batemans Shelf, Twofold Shelf and Eastern Tasmanian bioregions. These are among 65 Australian marine bioregions that provide a framework for consistent, ecologically based environmental planning (IMCRA 1998). These regional divisions also represent appropriate spatially explicit domains for the consideration and development of climate change adaptation strategies.

3.3.2 - Oceanographic habitat modelling

An oceanographic habitat model for kingfish from eastern Australia was recently developed to test for climate-driven shifts in suitable environmental habitat over the period January 1996 – July 2017 (Champion *et al.* 2018b). This model predicts the spatial distribution of suitable kingfish habitat as a function of sea surface temperature, sea level anomaly and eddy kinetic energy, which are significant predictors of kingfish occurrence (Brodie *et al.* 2015;

Champion *et al.* 2018b). To create this model, kingfish occurrence records, or presence points, were obtained from a recreational fisheries catch-and-release tagging program administered by the New South Wales Department of Primary Industries. Spatial and temporal independence among these data was satisfied by retaining only presence points from a unique day and location, and retaining only those that were greater than 0.1 degree (~ 20 km) apart (Figure 2.2; Brodie *et al*. 2015). Following these procedures, and restricting the dataset from 1996 – 2015 to match the availability of satellite-derived environmental covariates, a total of 1,203 kingfish presence points were available for analysis. These presence points were combined with a large number (20,000) of pseudo-absence points randomly generated throughout the study area to categories unsuitable environmental habitat for kingfish (Barbet-Massin *et al.* 2012). A suite of explanatory oceanographic variables of likely importance to coastal-pelagic fishes (Hobday and Hartog 2014) were matched to the resulting set of presence and pseudo-absence data using the Spatial Dynamics Ocean Data Explorer (Hartog *et al*., 2011). These included sea surface temperature (SST), sea level anomaly (SLA), dissolved oxygen (DO) and eddy kinetic energy (EKE). In this region, satellite-based chlorophyll estimates are significantly correlated with SST and have incomplete spatial and temporal coverage so were not matched to presence and pseudo-absence data. Collinearity among predictor variables generally has a negative effect on model performance (Zuur *et al.* 2007) and was assessed using pair plots and Spearman rank correlation coefficients. A strong correlation between SST and DO (r = -0.77) resulted in the removal of DO from the set of oceanographic predictors in favour of SST, which is known to strongly influence the distribution of kingfish (Brodie *et al.* 2015).

Kingfish oceanographic habitat preference was then described by applying generalised additive mixed modelling (GAMM) using the logistic link function to relate the binomially distributed response variable (i.e. presence or pseudo-absence) to oceanographic predictors. In the absence

of information on fishing effort in the tagging database, calendar year was included as a random effect to account for inter-annual variability in catch per unit effort. Following a forward model selection procedure and cross-validation process the optimal habitat suitability model has the form:

$$Response = s(SST) + SLA + s(EKE) + (1|Year) \quad (1)$$

where *Response* is a measure of kingfish habitat suitability (between 0 – 1) modelled as a function of *SST*, *SLA* and *EKE*, with *Year* included as a random term. Penalized regression spline type smoothers of moderate rank are denoted by *s*. A full description of model selection and evaluation procedures used to specify and test the accuracy of this habitat suitability model are provided in Chapter 2 of this thesis.

3.3.3 - Suitable vs. unsuitable oceanographic habitat

Measures of species environmental habitat suitability are commonly produced on continuous scales (i.e. 0 – 1), and converting these into categorical projections requires a threshold habitat suitability value to differentiate between suitable and unsuitable habitats (Liu *et al.* 2005). A threshold of 0.5 is widely used in ecology (Bailey *et al.* 2002; Manel *et al.* 1999; Stockwell and Peterson 2002), despite often being an arbitrary selection lacking ecological basis (Liu *et al.* 2005).

In this study, we take an objective, data-driven approach for identifying this value by aiming to maximise the agreement between observed and predicted distributions, which has been suggested as a robust alternative to assuming arbitrary values (e.g. 0.5; Liu *et al*. 2005). To do

so, kingfish occurrence records, independent of those used to train the habitat model, were extracted from the Atlas of Living Australia (http://www.ala.org.au/) and compared with spatial projections of modelled habitat. Only records from the period 2006 – 2016, and from a unique day and location within the spatial extent of the present study, were retained to assess habitat suitability values for these points. This was done to ensure habitat suitability values matched to Atlas of Living Australia data were predicted using the same environmental data sources used to generate future habitat projections (see section *3.3.4 - Past and future habitat* below). Subsequently, a total of 22 day-specific projections of kingfish oceanographic habitat were created with 0.1° spatial resolution, and habitat suitability values for grid cells containing independent occurrence records were extracted from each projections (Figure 3.1).

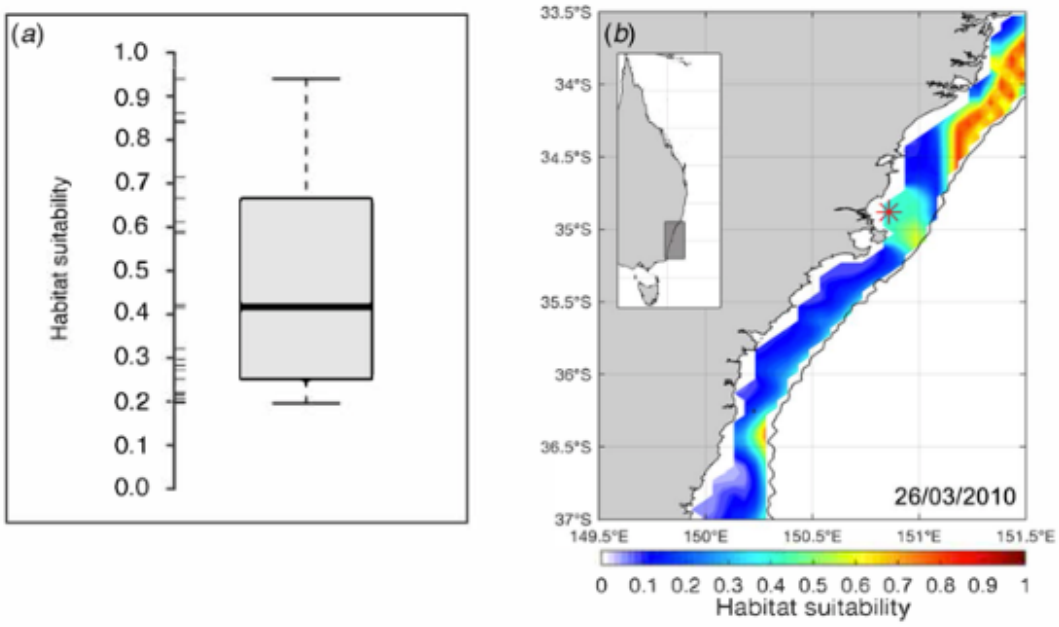


Figure 3.1. (*a*) Distribution of habitat suitability values from Atlas of Living Australia kingfish occurrence records (n = 22; min = 0.196) matched with day-specific habitat projections used to deferential between 'suitable' and 'unsuitable' oceanographic habitats (i.e. suitable ≥ 0.196 < unsuitable) for temporal persistence analyses. (*b*) Example of a day-specific kingfish habitat projection matched with an Atlas of Living Australia kingfish occurrence record (red asterisk) used to create the distribution in (*a*).

The minimum value (0.196) from the resulting dataset of suitable habitat values was adopted as the threshold to differentiate between suitable and unsuitable kingfish oceanographic habitats. This is likely to be a conservative estimate for suitable kingfish oceanographic habitat because our threshold value has been determined using only 22 observational data points. Regardless, the objective of this study was to quantify relative changes in the temporal persistence of suitable kingfish habitat through time, which can be achieved providing the threshold value used to convert continuous projections of habitat suitability into binary categories is held constant over the study period. For example, using lower threshold values would result in more habitat being included as 'suitable' and likely increase absolute values of regional temporal persistence, and vice-versa if higher threshold values are used. Therefore, absolute values for temporal persistence of suitable kingfish habitat (reported as months per year) within south-eastern Australian bioregions should be interpreted with care as these have been conservatively estimated. Instead, attention should be focused on relative trends in temporal habitat persistence through time, which remain robust regardless of the threshold value utilised. Our approach simply applies an objective, data-driven method for the differentiation of 'suitable' from 'unsuitable' kingfish oceanographic habitat. Doing so improves the agreement between observed and predicted distributions and the interpretability of results (Liu *et al.* 2005).

3.3.4 - Past and future habitat projections

Habitat projections for the period 1996 – 2016 were made using satellite-derived, monthly averages for oceanographic predictor variables. Specifically, these were SST from Advanced Very High Resolution Radiometer (AVHRR), SLA from synthetic temperature and salinity analyses (Ridgway and Dunn 2010) and EKE derived from from AVISO altimetry. Monthly averaged spatial surfaces for these variables were generated and interpolated to the largest common resolution (0.2°), and as a result all projections of kingfish oceanographic habitat for the period 1996 – 2016 were resolved to 0.2°.

Habitat projections for the period 2006 – 2040 were based on oceanographic variables available from the CSIRO Ocean Downscaling Project (hereafter 'CSIRO-Downscaling'). A global high-resolution (0.1°) ocean general circulation model (OGCM) is used to dynamically downscale climate changes in the 21st century derived from Coupled Model Intercomparison Project Phase 5 (CMIP5) climate models (Taylor *et al.* 2012). The OGCM is the Ocean Forecasting Australia Model Version 3 (Oke *et al.* 2013), based on version 4p1d of the GFDL Modular Ocean Model (Griffies *et al.* 2009), which is configured to have 0.1° grid spacing for all longitudes between 75°S and 75°N and 51 vertical layers. The global OGCM is integrated over the historical period (1979 – 2014) driven by 3-hourly Japanese 55-year Reanalysis (JRA-55; Kobayashi *et al*. 2015) through bulk formula. Details about model set-up of this historical experiment and validation with both in-situ and satellite observations are provided in Zhang *et al.* (2016). The model is further integrated from 2006 to 2101, driven by merged atmospheric forcing which includes a high-frequency (daily to interannual) part from current-day JRA-55 reanalysis and a long-term climate change part from the ensemble of 17 CMIP5 models under the Representative Concentration Pathway 8.5 (RCP 8.5) scenario. High-resolution (0.1°) model results provide downscaled climate change projections in the 21st century for all common ocean state variables including sea level, temperature and currents. Monthly averages for SST, SLA and EKE for kingfish oceanographic habitat projections were generated from daily model results of CSIRO-Downscaling.

Kingfish oceanographic habitat projections made using satellite-derived and modelled oceanographic variables overlapped for the period 2006 – 2016. This period was used to compare the accuracy of future model-based habitat projections with those made using observed oceanographic conditions. To do so, correlations among monthly spatial projection matrices of kingfish habitat created using observed and modelled environmental predictors

were assessed. Pearson correlation coefficients and the statistical significance of these relationships were used to infer the accuracy of future habitat projections to the year 2040.

3.3.5 - Temporal persistence analysis

Monthly spatial projections of kingfish habitat were used to identify the presence or absence of suitable habitat within six southeast Australian marine bioregions from 1996 to 2040. The number of months per year that suitable habitat was present within each bioregion was subsequently calculated, and represents the temporal persistence of suitable kingfish oceanographic habitat. Trends in temporal habitat persistence through time were analysed individually for each bioregion using simple linear models to test if slopes significantly differed from zero. Because habitat projections for the periods 1996 – 2016 and 2006 – 2040 were based on different sources of environmental data, temporal persistence values derived for these periods are not directly comparable and separate models were fitted for each. Subsequently, models testing for trends in temporal habitat persistence from 1996 to 2016 reflect results of historical change, while those for the period 2006 – 2040 reflect predicted future outcomes. Residual plots were visualised for each linear model fitted to assess if the assumptions of normality and homogeneity of variance were satisfied.

Statistical analyses were undertaken using the R programming language (R Foundation for Statistical Computing, Vienna, Austria; see https://www.R-project.org/) with GAMMs fitted using the 'gamm4' package (ver. 0.2-4, S. Wood and F. Scheipl, see https://CRAN.R-project.org/package=gamm4). Generation of pseudo-absence points and spatial plotting was undertaken in the Matlab (ver. 9.2, The MathWorks, Inc., Natick, MA, USA) computing environment.

3.4 - Results

3.4.1 - Kingfish oceanographic habitat

The future distribution of kingfish oceanographic habitat on the continental shelf of south-eastern Australia is predicted to continue undergoing a poleward advance during the austral summer and autumn and an equatorward retreat during winter and spring (Figure 3.2). Past and future spatial projections of kingfish habitat were derived from simultaneous responses to multiple oceanographic variables. Specifically, SST and EKE are highly significant, non-linear predictors of oceanographic habitat suitability, while SLA has a marginally significant, positive linear effect (Table 2.3, Figure 2.5). The habitat model had good-to-high predictive skill when evaluated against observational data (Table 2.2), indicating that spatial projections based on SST, SLA and EKE are effective at describing suitable environmental conditions for kingfish from south-eastern Australia.

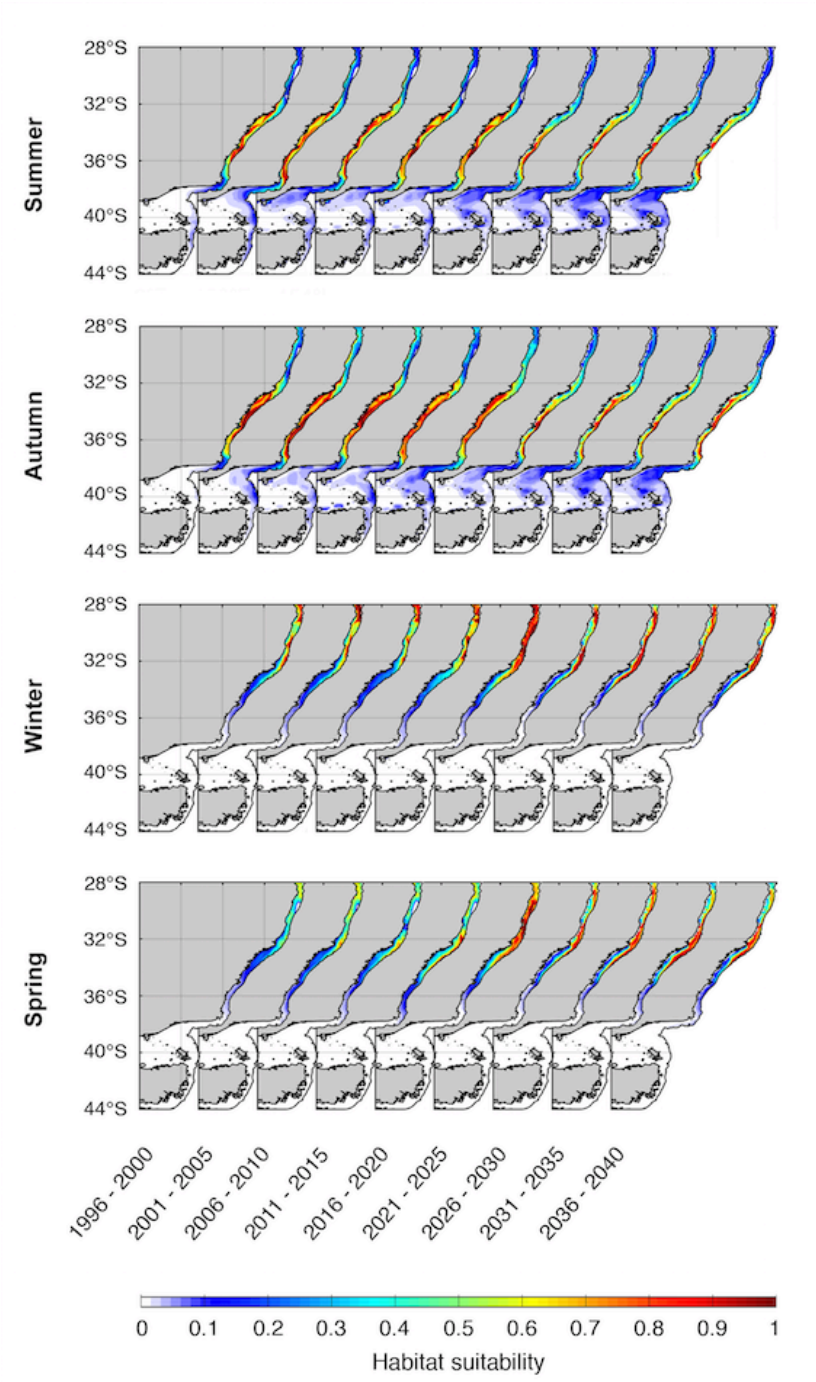


Figure 3.2. Spatial projections of kingfish oceanographic habitat suitability nearshore of the continental shelf break (200 m isobath) from 1996 – 2040. Habitat projections from 1996 – 2016 are based on satellite-observed environmental data and habitat projections from 2017 – 2040 are based on environmental data derived from oceanographic modelling forced under the Representative Concentration Pathway 8.5 ('business as usual') scenario. For graphical presentation, monthly spatial projections have been time-binned (5 years) and seasonally aggregated (Summer = December – February, Autumn = March – May, Winter = June – August, Spring = September – November).

3.4.2 - Evaluation of future habitat projections

Habitat projection matrices created using satellite-observed and modelled oceanographic environmental data for each month over the period 2006 – 2016 were significantly correlated at $\alpha = 0.01$ level. Pearson correlation coefficients for these comparisons ranged from $r = 0.51$ to $r = 0.85$ (Figure 3.3). These findings support the use of monthly kingfish oceanographic habitat projections using modelled oceanographic variables derived from CSIRO-Downscaling and forcing under RCP 8.5 to the year 2040.

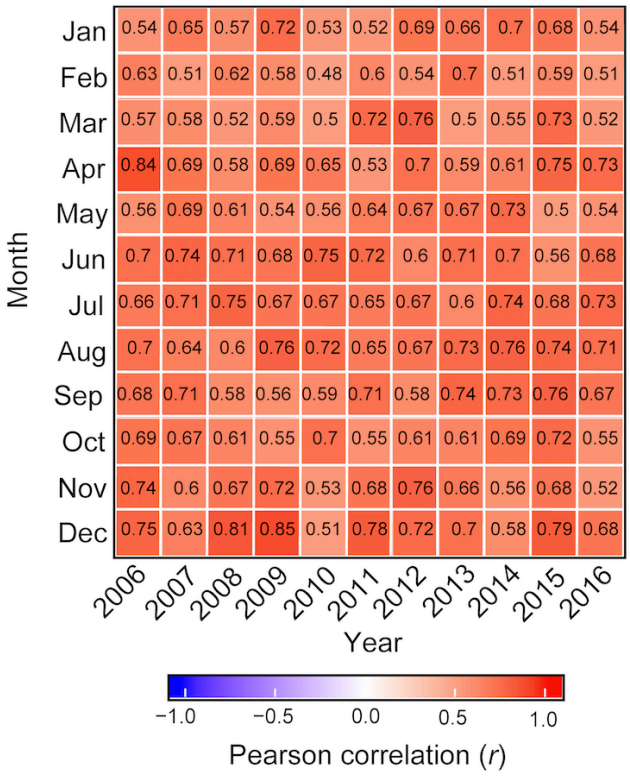


Figure 3.3. Pearson correlation coefficients for relationships between kingfish oceanographic habitat projections utilising satellite-observed environmental predictors *vs.* habitat projections utilising oceanographic modelling forced under the Representative Concentration Pathway 8.5 scenario from 2006 – 2016. All monthly correlations exceed $r = 0.5$ and are statistically significant at $\alpha = 0.01$ level.

3.4.3 - Temporal persistence of suitable habitat

Significant shifts in temporal persistence of suitable kingfish oceanographic habitat are expected within four out of six south-eastern Australian marine bioregions assessed over the period 2006 – 2040 (Figure 3.4). A significant decline in habitat persistence is predicted for the northernmost Tweed-Morton bioregion over this period (Figure 3.5a), while significant increases in temporal persistence of suitable habitat is expected for Batemans Shelf (Figure 3.5b), Twofold Shelf (Figure 3.5c) and Eastern Tasmanian (Figure 3.5d) bioregions. A significant increase in temporal persistence of suitable kingfish habitat within the Eastern Tasmanian bioregion was also identified for the period 1996 – 2016 (Figure 3.5d).

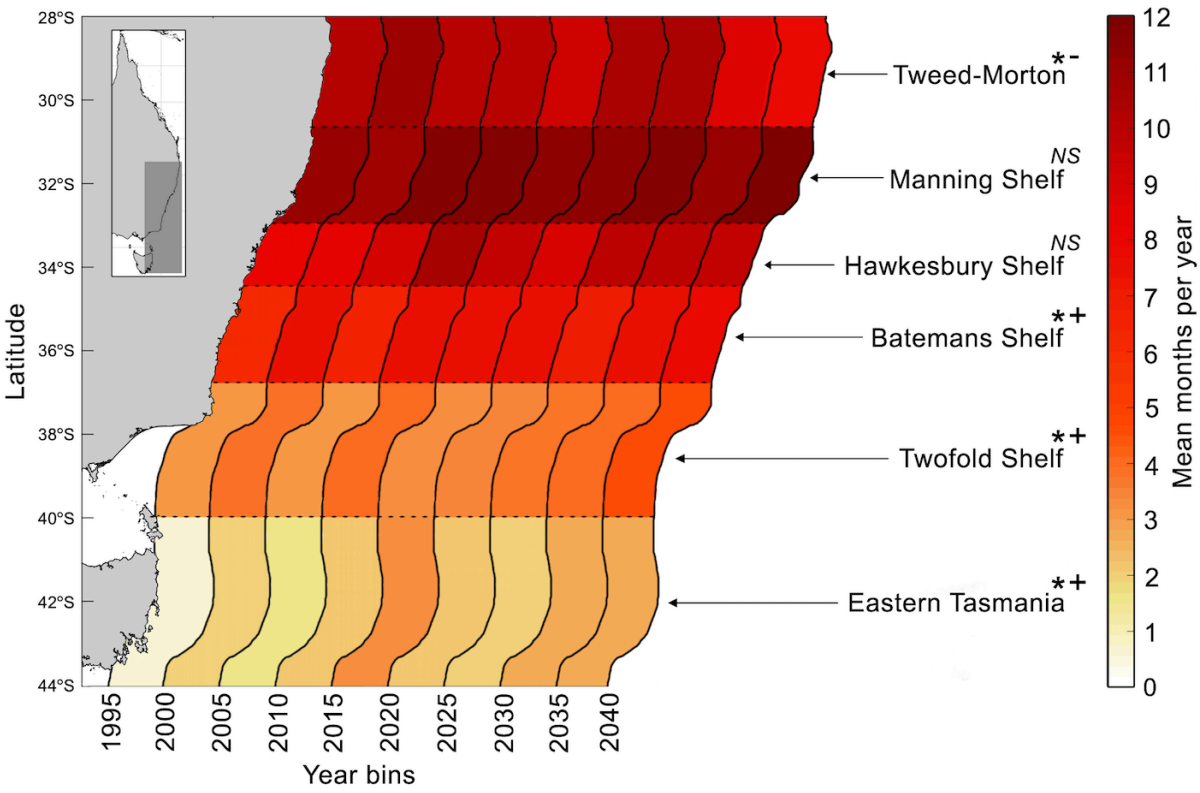


Figure 3.4. Temporal persistence (months per year) of suitable kingfish oceanographic habitat within south-eastern Australian marine bioregions through time. Statistically significant trends in temporal habitat persistence are indicated by asterisks (*) next to bioregion names, where positive symbols (+) indicate significant increases in habitat persistence and negative symbols (-) indicate a significant decrease in habitat persistence through time. *NS* denotes non-significance. Statistical analyses are based on monthly spatial projections of suitable kingfish oceanographic habitat from 2006 – 2040 under the RCP 8.5 scenario, and are detailed in Figure 3.5 for bioregions displaying significant trends.

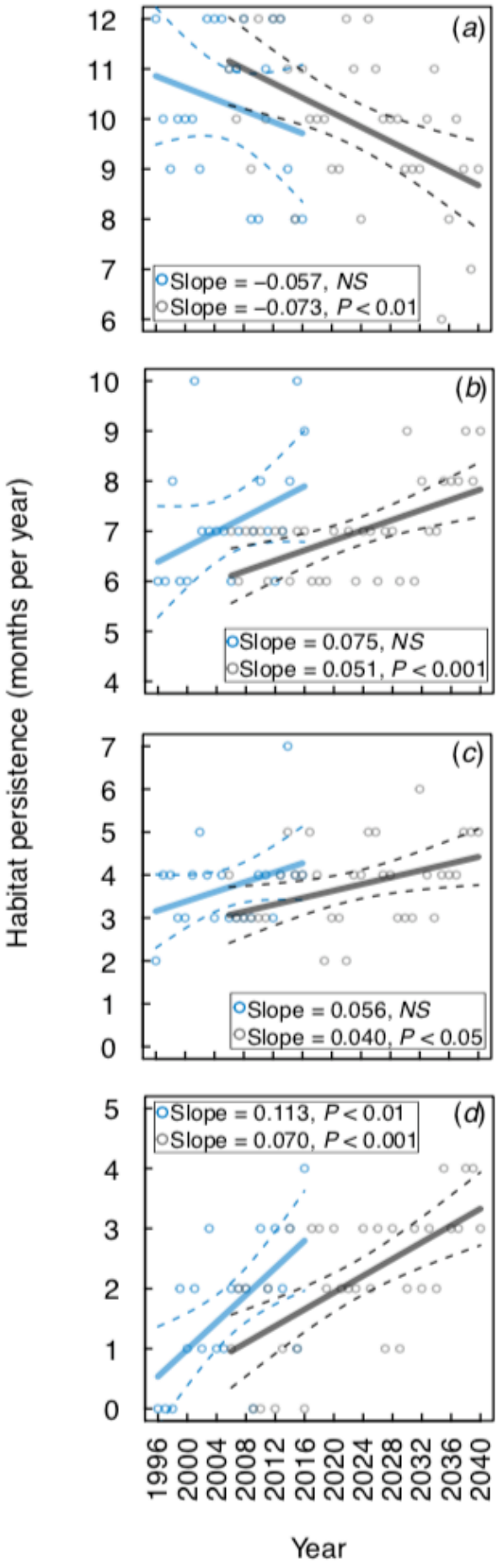


Figure 3.5. Temporal trends in the persistence of suitable kingfish oceanographic habitat within (*a*) Tweed-Morton, (*b*) Batemans Shelf, (*c*) Twofold Shelf and (*d*) Eastern Tasmania marine bioregions. Blue data represent the temporal persistence of suitable kingfish habitat based on monthly spatial habitat projections utilising satellite-observed environmental predictors from 1996 – 2016, while grey data are derived from monthly spatial habitat projections utilising oceanographic modelling forced under the RCP 8.5 scenario from 2006 – 2040.

3.5 - Discussion

Predicting kingfish oceanographic habitat at monthly time steps using multiple environmental variables revealed significant shifts in the temporal persistence of suitable habitat within several marine bioregions from south-eastern Australia for the period 1996 – 2040. These results follow a latitudinal trend, where a significant decline in temporal habitat persistence is predicted for the northernmost (equatorward) bioregion assessed over the period 2006 – 2040, while significant increases in habitat persistence have been identified for the three southernmost (poleward) bioregions analysed over this period. The most rapid increase in temporal habitat persistence is predicted for the Eastern Tasmanian bioregion, which was the most poleward bioregion investigated.

Trends in temporal persistence of suitable kingfish habitat within bioregions, and variation among these trends, are accounted for by climate-driven effects on regional oceanography. The marine environment adjacent to south-eastern Australia is characterised by a dynamic oceanographic regime dominated by the EAC. The EAC strengthens and extends poleward during the austral summer and autumn, resulting in warmer waters extending south, before retreating equatorward during winter and spring (Suthers *et al.* 2011). In addition to this seasonal extension and contraction, increased wind stress over broad region of the South Pacific associated with climate change is driving a poleward advance of the EAC (Cai *et al.* 2005; Sloyan and O'Kane 2015). Consequently, SST off south-eastern Australia is increasing at a rate between three and four times the global average (Ridgway 2007). Because the effect of temperature on kingfish habitat suitability peaks at approximately 21°C, the poleward advance of relatively warm water carried by the EAC directly increases the suitability of high-latitude environments from south-eastern Australia for kingfish. The influence of the extending

EAC on the temporal persistence of kingfish habitat is therefore most pronounced in the Eastern Tasmanian bioregion, where SST is increasing at a rate of 2.28°C century^{-1} (Ridgway 2007). Conversely, the effect of temperature on kingfish habitat suitability becomes negative when greater than approximately 22°C. It is likely that the decline in temporal habitat persistence predicted for the northern Tweed-Morton bioregion will result from increased persistence of SST warmer than 22°C within this bioregion. Although SLA and EKE are also significant predictors of kingfish oceanographic habitat, the role of these variables in changes to kingfish habitat persistence is less clear. SLA has a positive linear effect on kingfish habitat suitability, indicating that kingfish occurrence is likely to be higher in convergence areas. Positive sea level anomalies generally favour the occurrence of pelagic fishes as these are characterised by relatively higher levels of biological productivity than regions of negative sea level anomaly, due to the pooling of oceanic water that entraps and entrains primary productivity, larval and schooling baitfishes (Suthers *et al.* 2011). Low EKE values generally having a positive effect on model parameters that declines at values greater than approximately 0.11 m^2 s^{-2}, suggesting kingfish generally select for habitats characterized by relatively low EKE. While increases in SLA and EKE are predicted for south-eastern Australia under future climate change (Zhang *et al.* 2017), shifts in habitat suitability for kingfish in coastal bioregions are most likely to be influenced by changes to SST relative to the unimodal effect of temperature on habitat suitability. While our analyses focus on the physical determinants of kingfish oceanographic habitat, biotic factors (e.g. prey availability) are likely to have an important effect on the realised distribution and temporal persistence of kingfish (Mellin *et al.* 2016). To extend the interpretation of our results from the oceanographic habitat for kingfish to the distribution of kingfish directly would also require consideration of climate-driven effects on, for example, the spatiotemporal distribution of important prey species.

Increased ecological opportunity for kingfish within Batemans Shelf, Twofold Shelf and Eastern Tasmanian bioregions may result from increasing annual persistence of suitable environmental habitat. For example, ocean warming occurring off eastern Tasmania (Ridgway 2007) has increased the proportion of winter months that exceed the thermal threshold for larval development of the poleward extending long-spined sea urchin *Centrostephanus rodgersii* (Ling *et al.* 2009). Increased temporal persistence of suitable thermal habitat for this species has contributed to its establishment within high-latitude ecosystems, resulting in increased grazing pressure on macroalgal beds (Ling and Johnson 2009). Similarly, increased seawater temperatures and/or intensifying boundary currents have been linked with increased abundances of tropical herbivorous fishes in temperate ecosystems globally (Vergés *et al.* 2014; Wernberg *et al.* 2016). While changes in abundance and biotic interactions are unknown for kingfish at the southern range edge of their distribution, recent photo-verified observations from 43.5°S have increased the poleward extent of this boundary by approximately 200 km from previous records (Stuart-Smith *et al.* 2016). These observations suggest that the significant increase in the temporal persistence of suitable habitat identified for eastern Tasmania between 1996 – 2016 may be allowing for the presence and persistence of kingfish at the poleward tip of continental Australia.

Social and economic opportunities associated with commercial, recreational and charter fisheries for kingfish from south-eastern Australia may be affected by predicted shifts in temporal habitat persistence between 2006 – 2040 (van Putten *et al.* 2015). Changes in fishing opportunity inferred from shifts in temporal habitat persistence for kingfish from south-eastern Australia concur with a global analysis of the effects of climate change marine fisheries catch potential (Cheung *et al.* 2010). Cheung *et al.* (2010) show that global fisheries catch potential is likely to increase between 30 – 70% in higher-latitude regions (i.e. the poleward bioregions

herein) and decline by approximately 40% in lower-latitude regions (i.e. the Tweed-Morton bioregion herein) under future climate change. Specifically, increases in catch potential are predicted at the poleward tips of continental shelf margins (Cheung *et al.* 2010), which is represented by the Eastern Tasmanian bioregion in the present study where temporal habitat persistence was found to be increasing most rapidly.

Temporal habitat persistence is directly relevant to climate change adaptation by fishers and managers of this resource. When faced with reduced fishing opportunity due to declining habitat persistence (i.e. in the Tweed-Morton bioregion), recreational anglers may adapt by travelling to fish different locations, fishing for longer each season or targeting different species (van Putten *et al.* 2017). Similarly, when fishing opportunity increases (i.e. in the Batemans Shelf, Twofold Shelf and Eastern Tasmania bioregions) anglers may choose to increase their effort to target novel species or financially invest in the fishery (van Putten *et al.* 2017). Greater willingness to implement behavioural adaptation is associated with increased opportunity, while fishers are less likely to adapt their behaviour when fishing opportunity is declining (van Putten *et al.* 2017). Therefore, anglers targeting kingfish within the Tweed-Morton bioregion may be less likely to adapt to shifts in the temporal persistence of suitable kingfish habitat compared with anglers in the three poleward bioregions where opportunity is increasing. Management approaches that aim to maximise increases in fishing opportunity associated with changes in temporal habitat persistence may further increase the willingness of fishers to implement behavioural adaptations. The seasonal deployment of anchored fish aggregation devices (FADs) is a possible approach to maximise fishing opportunity in bioregions where increased temporal persistence of suitable environmental habitat is predicted. FADs are known to effectively increase fishing opportunity for kingfish (Dempster 2004) and are currently deployed nearshore of the continental shelf break off New South Wales during summer months

(Folpp and Lowry 2006). This fisheries enhancement strategy could be extended to eastern Tasmania with future projections of the annual persistence of suitable oceanographic habitat for kingfish used to make decisions regarding the timing and duration of FAD deployments (Brodie *et al.* 2017).

Adaptation responses and the timing of their implementation are known to be influenced by how well resource users are informed of the changes happening around them (Hill *et al.* 2010; van Putten *et al.* 2017). Therefore, improving the quality of information available to stakeholder groups by ensuring it is relevant to their use of marine resources and presented at timescales applicable to decision making is critical for eliciting behavioural adaptation responses. Here, we provide stakeholders with specific information about the future effect of climate change on a focal species. This was achieved by quantifying the number of months per year that suitable habitat for kingfish persists within spatially explicit regions, which can be easily interpreted as the annual duration of suitable fishing conditions. Similar analyses could be tailored to develop adaptation approaches for a range of species under future climate change. Opportunities exist to examine future environmental change on known conflicts between the activities of marine users and habitats for key species (Hartog *et al.* 2011b; Hobday and Hartmann 2006; Howell *et al.* 2015). Specifically, analyses that test for climate-driven shifts in the spatiotemporal overlap of fishing operations and environmental habitats for species of high conservation value could identify and help to minimise such conflicts in the future (Hartog *et al.* 2011b; Lewison *et al.* 2004). Furthermore, demographic habitat suitability modelling (Brook *et al.* 2009; Franklin 2010), used to identify environmental conditions that are important for species' crucial life history stages (e.g. suitable spawning conditions), could be applied to assess the vulnerability of these habitats to climate change. Development of metrics that are applicable to affected stakeholder groups are important for communication and understanding

in order to reduce the vulnerability of marine users to climate change by creating capacity for behavioural adaptation that minimises loss and maximises opportunity.

- Chapter 4 -

Maximising the utility of bioelectrical impedance analysis for measuring fish condition requires identifying and controlling for sources of error [3]

4.1 – Abstract

Body condition indices are commonly used to represent the physiological status of fishes. Bioelectrical impedance analysis (BIA) has emerged as a rapid, nonlethal and cost-effective method for measuring fish condition and predicting proximate composition components, such as per cent fat. Measuring the condition of fish obtained from varied sources requires consideration of potential sources of error to ensure robust and comparable data are obtained. This is important when opportunistically applying BIA to assess fish condition for species that are logistically difficult to sample (e.g. large-bodied marine fishes), when different sampling methods are used, or where fish handling effects may confound condition comparisons. We experimentally tested the effects of five factors related to fish handling on an instantaneous body condition index (phase angle) measured using BIA. Using the coastal-pelagic yellowtail kingfish (*Seriola lalandi*) as a model species, we identified significant effects for four out of five factors tested; time since death, temperature of the tissue, removal of the gills and gastrointestinal tract, and the anatomic location for measurements. We thus propose protocol considerations when using BIA to opportunistically measure condition in fish obtained from varied sources. These sampling protocols for the robust application of BIA can maximise the utility of this approach for opportunistically measuring body condition in fish.

[3] **Chapter is in review**: Champion, C., Hobday, A. J., Pecl, G. T., and Tracey, S. R. Maximising the utility of bioelectrical impedance analysis for measuring fish condition requires identifying and controlling for sources of error. *Fisheries Research*, In Review.

4.2 - Introduction

Body condition indices in fish and fisheries research are widely used to infer physiological status (Murphy *et al.* 1990). Measures of fish condition can reveal important biological and ecological relationships, such as variation in growth and recruitment of spatially discrete stocks (Rätz and Lloret 2003) and the influence of abiotic factors on the physiology of fishes (Adams *et al.* 2018; Kjesbu *et al.* 2014). Given that environmental variables are known to influence fish condition (Willis and Hobday 2008), and that climate-driven oceanographic changes are rapidly occurring globally (Wu *et al.* 2012), body condition indices are a useful approach to assess species' responses to environmental change (Champion *et al.* 2019a; Miranda *et al.* 2019).

Researchers use either traditional (Murphy *et al.* 1990) or emerging methods (Hartman *et al.* 2015) for quantifying the physiological status of fishes. Traditional measures of fish condition, such as Fulton's K and relative weight (W_r), typically rely on deriving species-specific length–weight relationships and measuring individual deviations from expected values (Hampton, 1986). However, these measures have been criticised as inaccurate estimates of physiological status (Green 2001), subsequently casting doubt over their ecological relevance. For example, the tendency of fish to replace lipids with water when fatigued or losing energy (Love, 1970) is likely to mask any true reduction in body condition when total mass based condition estimates are applied (Hartman and Margraf 2008). Direct approaches for measuring body composition indices, such as per cent fat or energy content (e.g. bomb calorimetry), are effective but are not widely applicable due to expensive and labour intensive laboratory processing requirements and the need for fish to be euthanised (Vogt *et al.* 2002). Alternatively, novel electrical conductivity methods have emerged as promising techniques capable of

measuring the body condition of fishes quickly and nonlethally (Hartman *et al.* 2015). These techniques include total body electrical conductivity and bioelectrical impedance analysis (BIA), which rely on measuring the impedance of biological tissue to an imperceivably weak electrical current. Of these, BIA is particularly useful in fish and fisheries research because the instrument is portable and user-friendly (Cox and Hartman 2005), allowing measures of the electrical impedance of biological tissue under a wide range of field and laboratory conditions and for fish of varying morphologies (Hartman *et al.* 2015). Given that the majority of studies to date have applied BIA to anadromous fishes (e.g. Salmonids) or in aquaculture settings (Cox and Heintz 2009; Cox and Hartman 2005; Duncan *et al.* 2007), there is a need to investigate practical considerations for using BIA to measure the body condition of marine fishes in the field.

Deriving robust body condition data through the application of BIA in the field requires an understanding of potential sources of measurement error. Measurement error can arise from (1) incorrectly using the BIA instrument to take measurements or, (2) a combination of factors relating to how and when BIA measurements are taken, which may be unique to individual species or groups of closely related species. Past studies have indicated practices that are important for correctly utilising BIA tools (Hartman *et al.* 2015). These include blot drying fish prior to making contact with the BIA instrument's electrodes, the application of firm and steady pressure between electrodes and fish tissue in order to establish a strong electrical circuit, and placing fish on a nonconductive board to ensure that the electrical circuit is not affected by external conductive material (Cox and Hartman 2005; Hartman *et al.* 2015). However, additional sources of measurement error may arise from species-specific factors, such as the anatomic location that electrodes are placed on individuals when measuring biological impedance. For example, Cox and Heintz (2009) observed significant differences

between phase angle values (a body condition metric derived from BIA measurements detailed in the methods section of this chapter) taken along the dorsal and ventral sides of chum salmon (*Oncorhynchus keta*), suggesting that the anatomic location of BIA measurements should be consistent in studies undertaking comparative analyses. Temperature has also been shown to influence BIA measurements (Cox *et al.* 2011; Gudivaka *et al.* 1996). Specifically, phase angle values recorded for dead fish have been shown to increase as tissue temperature decreases (Cox and Heintz 2009). These findings suggest that controlling for the effects of ambient temperature on BIA measurements is likely to be an important consideration for field-based studies that aim to compare data from locations or times with varying environmental temperatures.

The nature of the sampling program being undertaken can also introduce error. Sampling dead individuals is common and, given that cells begin to break down post-mortem, another possible source of error is the time after death that measurements are taken (Cox *et al.* 2011). For example, BIA measurements taken at varying times since fish have been caught and killed may not be comparable due to the degradation of biological tissue post-mortem. Analysing Coho Salmon (*Oncorhynchus kisutch*), Cox *et al.* (2011) found that BIA measurements became significantly different from freshly sampled individuals after fish had been dead for nine hours (while being held on ice). This is likely to be an important source of error when applying BIA in fishery-dependent sampling programs, including citizen science initiatives that encourage the donation of samples from recreational or commercial fishers. This window of time is likely to be species-specific due to the influence of variation in fish physiology on BIA measurements. Subsequently, the development of robust field-sampling protocols requires information from experiments that quantitatively evaluate potential sources of error to ensure that BIA measurements taken on samples from varying sources are representative of the condition of live individuals and measurements are comparable.

Despite evidence that several sources of measurement error can confound comparative analyses of BIA data, assessing different sources of error for the purpose of informing the robust application of BIA remains ad hoc. Furthermore, past studies (e.g. those reviewed by Hartman *et al.* (2015)) have a strong focus on small-sized anadromous fishes in laboratory settings and the responses of medium-bodied marine fishes (~50-100 cm) in a field setting may vary. Experiments that test for sources of measurement error are an important step prior to field studies that seek apply BIA, particularly to samples donated by citizen scientists. This step is necessary to ensure that studies yield robust and comparable body condition data that can be used to address ecological hypotheses.

The objective of this study was to identify factors that introduce measurement error in field-based studies that seek to opportunistically apply BIA to samples not captured by the research team. This step should occur prior to undertaking a field study where fish of different processing history or style may be encountered. Utilising the medium sized coastal-pelagic yellowtail kingfish (*Seriola lalandi*), we tested the potential effects of: (1) time since death, (2) fish size, (3) gill and gastrointestinal tract removal, (4) anatomic location of measurement, and (5) temperature of tissue on an instantaneous body condition index (phase angle) that is derived from BIA measurements. The results of these experiments informed a protocol for obtaining comparable phase angle data when applying BIA to samples from varying origins. We seek to assist researchers and managers to develop robust sampling protocols for the field-based application of BIA to their species of interest.

4.3 - Methods

4.3.1 - Bioelectrical impedance analysis

Bioelectrical impedance analysis works by passing a high frequency current (50 kHz) of imperceptible amplitude (800 μA) through body tissue between signal and receiver electrodes that are either pressed against the skin or inserted less than 1 cm into body tissue (depending on the configuration of the BIA tool; Figure 4.1) to measure impedance (Cox and Hartman 2005). Impedance is the sum of two vectors of electrical current, resistance and reactance, which are measured directly by the BIA tool. Resistance and reactance values are indicative of physiology status and can be used to derive additional biologically relevant parameters using electrical equations. Resistance measures the ability of extracellular material to conduct electricity (Cox and Hartman 2005). This is achieved in BIA by using an electrical current that is incapable of passing through cellular membrane, due to the presence of the nonconductive lipid bilayer that is pressed between two conductive protein layers. Subsequently, resistance reflects extracellular material, such as fat, which is nonconductive and can be indicated by higher resistance values (Cox *et al.* 2011). Reactance is the ability of a substance to hold a charge and is used in BIA to measure opposition of the cellular lipid bilayer (capacitor) to an alternating current (Cox *et al.* 2011). Subsequently, reactance is a measure of the total volume of healthy cells, which is indicative of an individual's body condition (Kyle *et al.* 2004).

Figure 4.1. Bioelectrical impedance analysis (BIA) being applied to the ventral tissue of juvenile yellowtail kingfish (*Seriola lalandi*).

Multiple studies have demonstrated that the composition and condition of fish can be accurately measured with BIA using direct (i.e. resistance and reactance) and derived measures (Cox and Heintz 2009; Hartman *et al.* 2015). To date, the majority of studies applying BIA to fish have relied on developing correlative relationships between the electrical impedance of tissue and measures of proximate body composition, such as total fat, per cent ash and moisture content (Cox and Hartman 2005; Duncan *et al.* 2007; Hafs and Hartman 2011). While BIA is often proposed as a nonlethal method for determining body composition and condition, proximate analyses required for calibrating correlative models rely on euthanising a representative sample of individuals (Cox and Hartman 2005). Once the relationships are calibrated, there is no need to sacrifice more animals and estimates of proximate body composition and condition can be made in approximately the same time it takes to measure fish length. Guidelines for model calibration have been established by Hartman *et al.* (2015), who suggest that a minimum of 60 individuals are required for proximate composition analyses and biochemical assays to develop accurate predictive relationships. However, 60 samples may be a prohibitively high number for many species, for example in studies seeking to apply BIA

to threatened species or those that are logistically difficult to sample, such as medium to large bodied pelagic fishes. Furthermore, the calibration of predictive models requires sufficient variation in response metrics (e.g. per cent fat) that may not be attainable when opportunistically sampling wild fishes. It is also uncertain how applicable relationships between impedance measurements and proximate composition measures are to individuals sampled from different ecological and spatiotemporal contexts than those used to calibrate these relationships. Given the potential for BIA to be utilised for opportunistically measuring samples obtained from a range of sources (e.g. citizen scientists initiatives, recreational fishers, commercial landings), there is a need to investigate the application of BIA for instantaneously quantifying fish condition in the field and without model calibration.

4.3.2 - Electrical phase angle as a body condition index

Electrical phase angle is a metabolic condition index (Willis and Hobday 2008) that is determined by the angle between the two vector components of impedance (resistance and reactance) and is defined as:

$$\text{phase angle } (^\circ) = \left(\arctan\left(\frac{X_c}{R}\right)\right) \times \frac{180^\circ}{\pi} \quad (1)$$

where X_c is reactance (ohms) and R is resistance (ohms). Phase angle measurements ranges from 0° to 90°, where higher values indicate good body condition due to high readings of X_c that are indicative of large quantities of intact cell membranes (Foster and Lukaski 1996).

Unlike body composition indices linked to BIA measurements (e.g. per cent fat), phase angle values can be instantaneously derived from resistance and reactance measurements and avoids

the need to euthanise a representative sample of individuals to calibrate regression equations (Cox and Hartman 2005). The use of phase angle instead of regression analysis for describing composition variables has become common in medical fields because phase angle is linked to metabolic rate and nutritional status, and can thus be used as a direct measure of body condition (Barbosa-Silva *et al.* 2003). In pelagic fish, Willis and Hobday (2008) used phase angle data to describe the body condition of southern bluefin tuna (*Thunnus maccoyii*) across years. Furthermore, Cox and Heintz (2009) found that phase angle was effective in differentiating between states of body condition in a variety of salmonids, where angles < 15° indicated fish in poor condition and angles > 15° indicated fish that were in relatively good condition. Therefore, phase angle is a promising metric as it provides an informative measure of fish condition that is instantaneous, nonlethal and does not require model calibration, thus eliminating regression error.

4.3.3 - Sampling of study species

To assess for potential source of error that may influence phase angle values measured during opportunistic field-based sampling, yellowtail kingfish (*Seriola lalandi*; hereafter 'kingfish') were sampled from south-eastern Australia using hook-and-line fishing between November 2016 and February 2019 for experimental analyses. Kingfish were chosen so that these experimental results could be used to inform a broader ecological study that aimed to measure the body condition of this species across a gradient of oceanographic habitat suitability (Champion *et al.* 2018). Kingfish from south-eastern Australia represent a single, genetically distinct population (Miller *et al.* 2011) with a distribution that is influenced by oceanographic variables, including sea surface temperature, sea level anomaly and current velocity (Brodie *et al.* 2015; Champion *et al.* 2018b). This species is targeted in several eastern Australian

fisheries, where the estimated annual recreational catch exceeds the average annual commercial catch (Henry and Lyle 2003; Lowry *et al*., 2016). Therefore, kingfish are representative of species' that may be donated by recreational fishers to scientific research projects seeking to quantify fish condition.

4.3.4 - Experiments

Experiment 1 – time since death

Variation in the time between capture (fish death) and when BIA measurements are taken may compromise accurate body condition comparisons (Cox *et al.* 2011). To test the effect of time since the death of fish on phase angle measurements, kingfish (n = 46) were caught by hook-and-line fishing, killed via ikejime, and held on ice and subjected to repeated phase angle measurements that were taken at 5-hour intervals for a period of 120 hours. Kingfish were caught over three consecutive austral summer seasons (December – February) and this experiment was repeated on three separate occasions to maximise sample size and due to logistical constraints associated with holding more than ~15 individuals on ice simultaneously. Preliminary data suggested that significant differences in phase angle measurements were apparent within the first 48 hours of fish being killed and held on ice, so measurements were taken at 10-hour intervals after fish had been repeatedly measured at 5-hour intervals for the first 70 hours of the experiment. All fish were covered in ice and kept in a 200-litre ice box, as is common practice when kingfish are caught in commercial and recreational fisheries. Phase angle measurements were taken along the dorsal musculature of kingfish (location A, Figure 4.2) placed in a left-facing orientation on a nonconductive polyethylene board. Fish were removed from the ice box for a period of 10 – 30 seconds for each phase angle measurement.

A TP20 digital thermometer (ThermPro, Toronto, Canada) was placed inside the ice box and readings were recorded 5-hourly in conjunction with BIA measurements to ensure that temperature remained constant throughout the duration of the experiment. Fresh ice was applied when necessary in order to maintain a consistent temperature (5°C ± 0.5°C) irrespective of the outside ambient temperature.

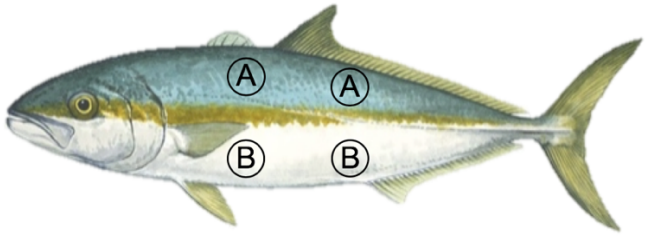


Figure 4.2. Anatomical locations for placing electrodes when taking BIA measurements on kingfish, where A denotes the placement of signal and receiver electrodes along the dorsal musculature, and B denotes the placement of signal and receiver electrodes along the ventral tissue of fish. Image credit: Peter Gouldthorpe (DPIPWE).

A linear mixed effects modelling approach was applied to assess for an effect of time after death on phase angle measurements. Initially, a simple linear model was applied and the residuals of this fit plotted against the factor 'fish ID' (i.e. a unique number assigned to each individual) to investigate the need to account for individual variation in phase angle measurements utilising a mixed effects modelling approach. This comparison revealed a clear pattern in residual variation (Figure 4.3), justifying the inclusion of fish ID as a random term to reduce the influence of individual variation in phase angle measurements on the fitted values of the model (Zuur *et al.* 2013).

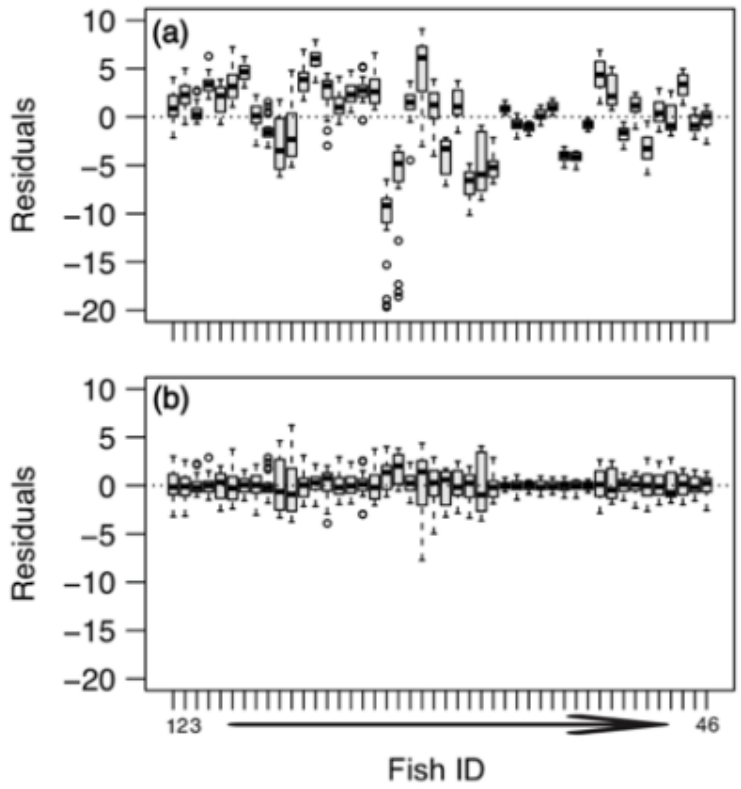


Figure 4.3. Distribution of residuals plotted against the factor 'fish ID' from (a) the simple linear model fitted to kingfish body condition data (phase angle) repeatedly measured at 5 – 10 hour intervals for a period of 120 hours, and (b) the linear mixed effects model fitted to the same data that incorporated fish ID as a random effect. Residuals of the linear mixed effects model are evenly distributed around zero, indicating that incorporating fish ID as a random effect improved model fit and assisted in satisfying the assumption of homogeneity of variance.

Tukey's honestly significant difference (HSD) post-hoc tests were applied to identify the time at which fish death began to significantly affect phase angle measurements. This test treated 'time after death' as a categorical variable and tested for significant differences between phase angle measurements taken at time = 0 (i.e. the time of death) and all subsequent time points when phase angle measurements were taken during the experiment. Phase angle measurements taken after kingfish had been held on ice for 5 hours were also compared with measurements taken at all subsequent time points. This was done to account for the potential effects of the temperature of fish tissue on phase angle measurements (Hartman *et al.* 2011), which varied

between measurement taken at time = 0 hours (i.e. freshly caught fish) and time = 5 hours (i.e. 5 hours spent on ice).

Experiment 2 – temperature effects

Previous studies have found that approximately 10°C of temperature change can significant affect BIA measurements (Hafs and Hartman 2015; Hartman *et al.* 2011). To assess if this trend was consistent for phase angle measurements taken on kingfish, five individuals were killed and placed on ice with the probe of a TP20 digital thermometer (ThermPro, Toronto, Canada) inserted 2 cm into the dorsal musculature of each individual. Temperature and phase angle measurements were taken at 10-minute intervals over a period of 2 hours. To test for an effect of time after death on phase angle measurements, a linear mixed effects modelling approach was applied to repeated measures data recorded for each individual throughout the duration of the experiment. Initially, a simple linear model was applied and the residuals of this fit plotted against the factor 'fish ID' (i.e. a unique number assigned to each individual) to investigate the need to included random slopes to account for individual variation in phase angle measurements. This comparison revealed a clear pattern in residual variation that was accounted for when fish ID was included as a random term in the model (Figure 4.4), which reduced the influence of individual variation in phase angle measurements on the fitted values of the model (Zuur *et al.* 2013).

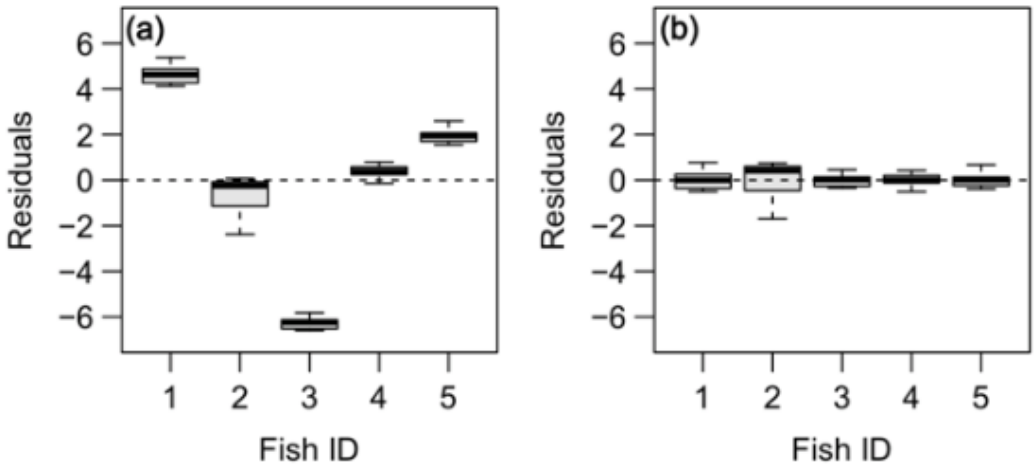


Figure 4.4. Distribution of residuals plotted against the factor 'fish ID' from (a) the simple linear model comparing tissue temperature change on phase angle measurements repeatedly taken along the dorsal musculature of 5 yellowtail kingfish at 10-minute intervals for a period of two hours, and (b) the linear mixed effects model fitted to the same data that incorporated fish ID as a random effect. Residuals of the linear mixed effects model are evenly distributed around zero, indicating that incorporating fish ID as a random effect improved model fit and assisted in satisfying the assumption of homogeneity of variance.

Experiment 3 – fish size

Fish size may confound body condition comparisons using BIA due to potential ontogenetic changes in the body composition of fishes (Pilati and Vanni 2007). To test for a relationship between fish size and phase angle, measurements were taken on kingfish (n = 98) that ranged from 29 – 127 cm FL and 0.41 – 20.1 kg along the dorsal musculature (location A, Figure 4.2) of individuals place in a left-facing orientation on a nonconductive polyethylene board. Because variation in environmental temperature has been shown to influence BIA measurements (Hartman *et al.* 2011), all fish were held on ice for 60 minutes prior to measurement to control for the potentially confounding effects of temperature on phase angle measurements. Relationships between electrical phase angle measurements and the length and

weight of kingfish were analysed using simple linear models to test if slopes significantly differed from zero.

Experiment 4 – gilled and gutted fish

Removing the gills and gastrointestinal tract of fish is common practice in recreational and commercial fisheries to preserve seafood quality and this procedure is likely to be encountered when applying BIA to samples opportunistically provided by fishers. To test for an effect of removing the gills and gastrointestinal tract on phase angle values, BIA measurements were taken along the dorsal musculature and ventral tissue (locations A and B, respectively, Figure 4.2) of kingfish (n = 11) before and after the removal of these tissues. Recently caught kingfish were held on ice for 60 minutes prior to measurement to control for the potential influence of temperature variation on phase angle values. All measurements were taken on a nonconductive polyethylene board with fish in a left-facing orientation. Paired sample t-tests were applied to assess if phase angle measurements were significantly affected by the removal of the gills and gastrointestinal tract. Separate analyses were applied to phase angle data taken along the dorsal musculature and ventral tissue of kingfish to control for potential differences due to the anatomic location of measurements (Cox *et al.* 2011).

Experiment 5 – anatomic location of measurement

The anatomic location of signal and receiver electrodes has been shown to influence BIA readings in pink salmon (*Oncorhynchus gorbuscha*; n = 5, mean fork length=49.4 cm, SD=0.9cm) (Cox *et al.* 2011). To test if this effect is consistent in the medium-bodied, coastal-pelagic kingfish, we compared phase angle measurements taken along the dorsal musculature

and ventral tissue of individual kingfish ranging from 42 – 127 cm FL and 1.1 – 20.1 kg (n = 25). All fish were measured in a left-facing orientation on a nonconductive polyethylene board after being held of ice for 60 minutes following death. The BIA unit that was used had a fixed distanced (10 cm) between signal and receiver electrodes and this desistance was therefore consistent for measurements taken at different locations. A paired t-test was applied to assess if phase angle measurements were significantly affected by the anatomic location of electrodes.

All BIA measurements were taken using the Seafood Analytics Certified Quality Reader (CQ Foods, Inc., Clinton Township, MI, USA) by PhD candidate Curtis Champion, as user experience can also affect BIA readings (Cox *et al.* 2011). Data from all experiments were analysed using the R programming language (R Core Team 2017). For all analyses, diagnostic plots were visualised to assess if the assumptions of normality and homogeneity of variance were satisfied. Kingfish were sampled in accordance with the University of Tasmania's Animal Care and Ethics approval number A0016150.

4.4 Results

4.4.1 - Experiment 1 – time since death

Phase angle measurements taken along the dorsal musculature of kingfish that were held on ice declined at a rate of 0.085 degrees hour^{-1} (0.081-0.088 95% CI; $t_{1,916}$ = -48.4, P < 0.001; parameters for fixed component of the linear mixed effects model: int = 31.239, slope = −0.085; intraclass correlation coefficient: Fish ID = 0.779). Tukey's HSD post-hoc tests revealed that phase angle measurements were significantly different between kingfish that had been held on ice for 20 hours and kingfish measured at the time of death (i.e. time since death = 0 hours; P = 0.038), and this difference became increasingly significant as time since death increased beyond 20 hours (Figure 4.5). Comparisons between repeated phase angle measurements taken on kingfish that had been held on ice for 5 hours and measurements taken at all subsequent time points also identified that significant differences occurred after 20 hours (P = 0.031).

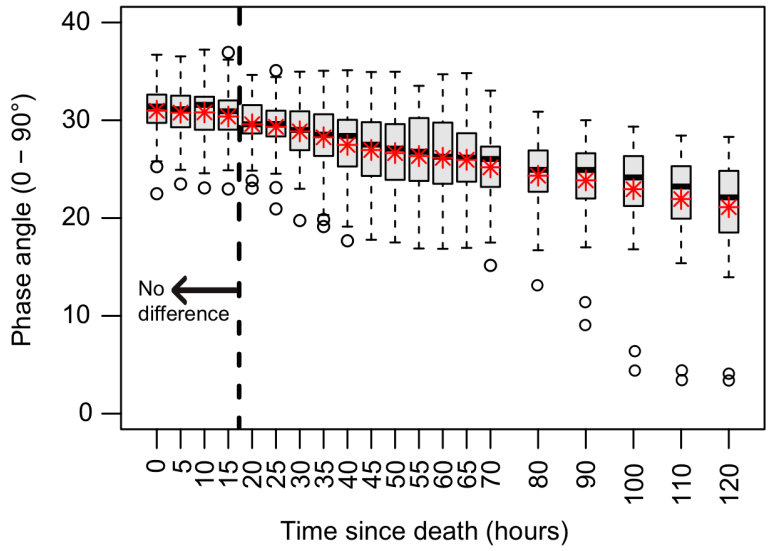


Figure 4.5. Boxplots summarising changes in phase angle values measured along the dorsal musculature of kingfish (n = 46) that were repeatedly measured over a period of 120 hours while being held on ice. Red asterisks denote mean values.

4.4.2 - Experiment 2 – temperature effects

The temperature of kingfish tissue was found to have a significant negative effect on phase angle measurements ($t_{1,56}$ = -11.58, P = 0.008; fixed components of the linear mixed effects model: int = 28.10, slope = −0.11; intraclass correlation coefficient: Fish ID = 0.986). Phase angle values were found to stabilise at temperatures less than approximately 5°C, or after being held on ice for approximately 60 minutes (Figure 4.9).

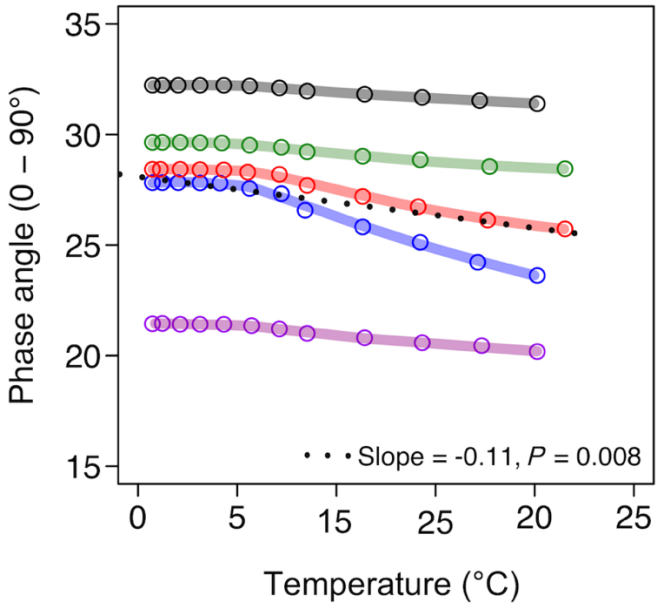


Figure 4.9. Effect of temperature change on phase angle data repeatedly measured along the dorsal musculature of 5 yellowtail kingfish at 10-minute intervals for a period of two hours. Coloured data represents individual fish and the black dashed line denotes the fixed slope of the linear mixed effects model.

4.4.3 - Experiment 3 – fish size

Linear regression analysis showed no significant relationship between phase angle measurements and the length or weight of kingfish (length: $F_{1, 96} = 0.168$, $P = 0.68$, $r^2 < 0.01$, Figure 4.6a; weight: $F_{1, 96} = 0.248$, $P = 0.62$, $r^2 < 0.01$, Figure 4.6b).

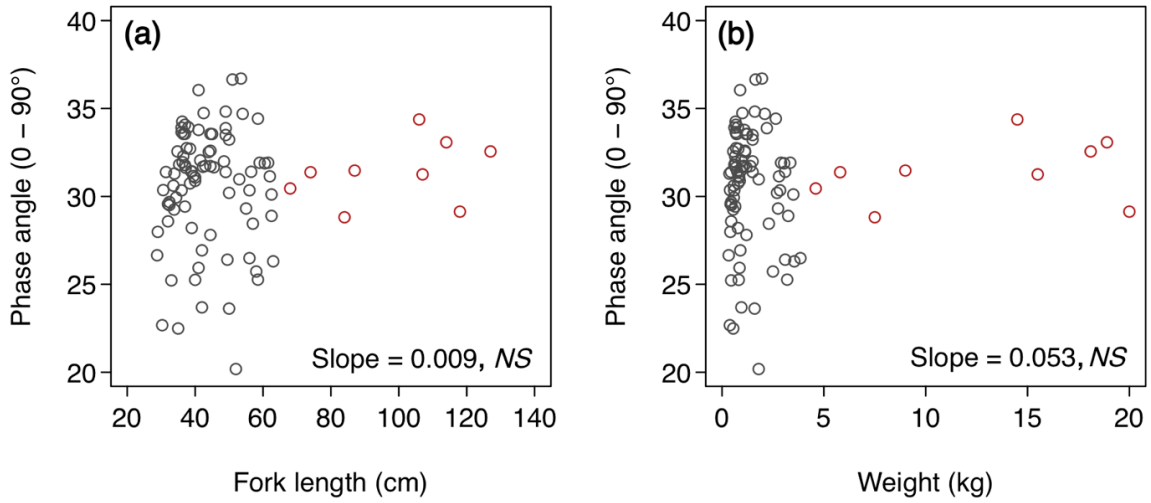


Figure 4.6. Relationships between fish size (a: fork length, and b: weight) and phase angle measurements taken along the dorsal musculature of kingfish ($n = 98$) that were held on ice for 60 minutes post-mortem. Grey data points represent juvenile kingfish and red data points represent reproductively mature individuals (determined through visual inspection of gonads).

4.4.4 - Experiment 4 – gilled and gutted fish

Phase angle measurements were significantly reduced due to the removal of the gills and gastrointestinal tract of kingfish (Figure 4.7). Specifically, the removal of the gills and gastrointestinal tract resulted in significant declines in phase angle measurements taken along both the dorsal musculature (paired sample *t*-test: $t_{10} = 9.99$, $P < 0.001$) and ventral tissue (paired sample *t*-test: $t_{10} = 11.99$, $P < 0.001$) of kingfish. Larger reductions in phase angle data were recorded for measurements taken along the ventral tissue of kingfish (Δ mean phase angle = -7.3) when compared with measurements taken along the dorsal musculature (Δ mean phase angle = -3.2).

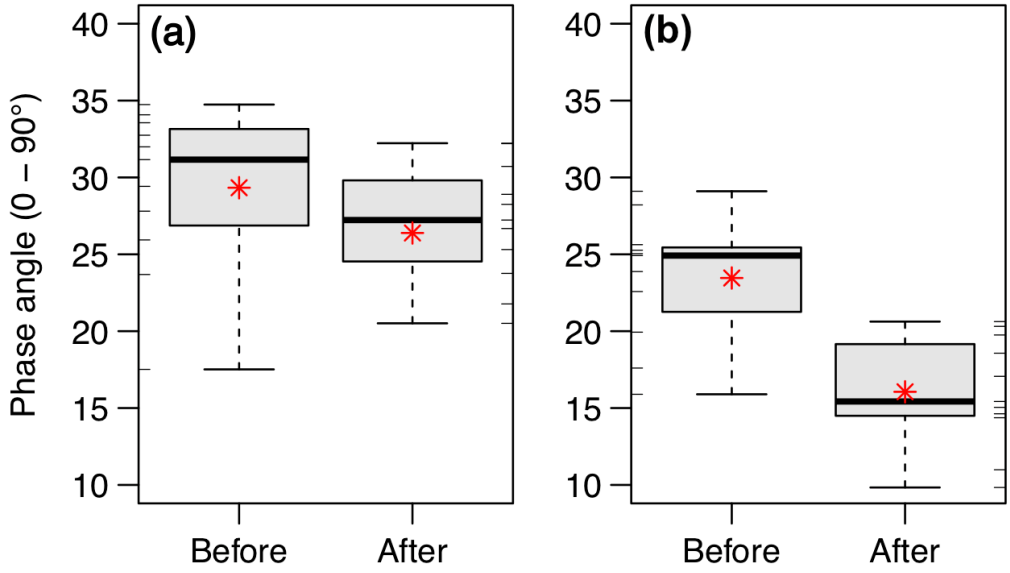


Figure 4.7. Boxplots summarising the distribution of phase angle measurements taken along (a) the dorsal musculature and (b) ventral tissue of kingfish (n = 11) before and after removal of the gills and gastrointestinal tract. Rugs on y-axes indicate phase angle values and red asterisks denote mean values.

4.4.5 - Experiment 5 – anatomic location of measurement

Phase angle values were dependent on the anatomic location of measurement (Figure 4.8). Specifically, phase angle was significantly higher when measured across the dorsal musculature of kingfish when compared to measurements taken across the ventral tissue of individuals (paired sample t-test: $t_{24} = 9.91$, $P < 0.001$).

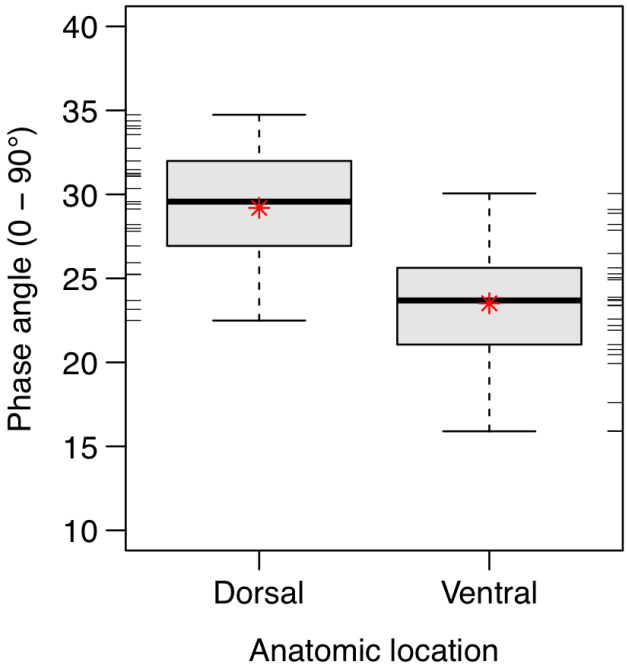


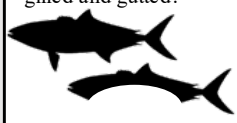
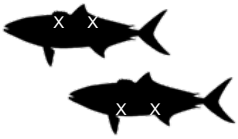
Figure 4.8. Boxplots summarising the distribution of electrical phase angle values measured across the dorsal musculature and ventral tissue of kingfish (n = 25). Rugs on y-axes indicate phase angle values and red asterisks denote mean values.

4.5 - Discussion

Testing for potential sources of measurement error is a crucial step in assessing the utility of novel research tools and for developing sampling protocols that yield comparable data. As interest in the application of BIA to fish continues to increase (Hartman *et al.* 2015), practical approaches to control for sources of variation are essential to ensure that BIA can be widely applied as a low cost, instantaneous and nonlethal approach for measuring fish condition. For example, blot drying and measuring fish on a nonconductive board is a standard practices for avoiding measurement error that should be adopted in all applications of BIA to fish and fisheries research (Cox and Hartman 2005). Given that BIA is well-suited for instantaneously and nonlethally assessing fish condition (Willis and Hobday 2008), our experiments focused on factors that may influence the application of BIA in the field and to

species that are difficult to obtain for traditional condition or proximate composition analyses (e.g. medium-sized pelagic fishes). While these experiments demonstrate factors that can confound comparisons of phase angle data that are opportunistically collected from different sources, they also highlight practical measures to effectively control for sources of variation. Here we place our results in the context of protocol considerations for opportunistically deriving comparable phase angle measurements from sources where fish handling differences may influence data quality (Table 4.1).

Table 4.1. Key considerations, viable solutions and examples for deriving robust and comparable phase angle data (referred to as 'condition measurements' within table) from varied sources based on experiments undertaken in this Chapter and from published literature.

	Consideration	Viable solution	Supporting evidence	Example in practice
Step 1	How long after fish death can accurate condition measurements be taken? 	Time since death affects condition measurements. Measurements taken within approximately 10 hours of fish death, provided fish are held on ice, should yield robust data.	Cox and Heintz, 2009 Cox et al., 2011 *Experiment 1* herein	Comparable condition measures were taken on kingfish (*Seriola lalandi*) between 0 and 15 hours since death while fish were held on ice (Champion et al., 2019).
Step 2	Will temperature affect condition measurements? 	Temperature affects condition measurements. Following capture and death, icing fish for short periods of time (e.g. 1 hour) prior to measurement can control for this effect.	Cox and Heintz, 2009 Cox et al., 2011 Hartman et al., 2011 Stolarski et al., 2014 *Experiment 5* herein	To yield comparable data, temperature effects have been controlled for by icing fish for 1 hour before taking condition measurements (Champion et al., 2019).
Step 3	Are condition measurements taken on whole fish comparable with fish that have been gilled and gutted? 	Condition measurements taken on whole fish are unlikely to be comparable with fish that have been gilled and gutted. Researchers should aim to compare measurements taken on whole fish only.	*Experiment 3* herein	In a comparison of the body condition of kingfish (*Seriola lalandi*) from eastern Australia, only whole fish were selected for sampling (Champion et al., 2019).
Step 4	Does the anatomic location of measurement affect condition data? 	Condition measurements taken at varying anatomic locations are unlikely to be comparable and a standardised location should be used.	Cox and Heintz, 2009 Cox et al., 2011 Hafs and Hartman, 2011 *Experiment 4* herein	Differences in impedance measurements taken at varying anatomic locations are known (e.g. Hafs and Hartman, 2011), and studies applying BIA commonly standardise the anatomic location of measurement (e.g. Stolarski et al., 2014).

4.5.1 - How long after death can comparable phase angle measurements be taken?

Our results indicate that phase angle measurements taken along the dorsal musculature of kingfish did not significantly change in fish that were placed on ice for 15 hours or less. These findings are comparable with those of Cox and Heintz (2009), who did not find an effect

of time on phase angle measurements taken on juvenile coho salmon (*Oncorhynchus kisutch*) within 12 hours of death. Similarly, Cox *et al.* (2011) also investigated the effect of time since death on coho salmon and found that both vector components of impendence, resistance and reactance, can be reliably measured within 9 hours of death provided fish are held on ice. The reduction in phase angle values through time can be attributed to the effects of rigor mortis (muscle contraction) on the integrity of cell membranes, which results in their degradation and the subsequent release of electrolytes and water into extracellular space (Martinsen *et al.* 2000). This process affects the ratio of intact cell membrane to extracellular material within fish tissue, which is used to calculate phase angle, and ultimately results in a negative relationship between time since death and phase angle values. Because icing fish delays post-mortem rigor mortis and subsequent tissue breakdown (Orr 1920), emphasis should be placed on the importance of icing fish immediately following death to maximise opportunities to accurately measure fish condition using BIA (Cox and Heintz 2009). Importantly, our results highlight that when fish are placed on ice following capture, an adequate amount of time is likely to be available to researchers to enact the logistics required to opportunistically sampling fish caught by recreational or commercial fishers (e.g. up to 15 hours for kingfish).

4.5.2 - Does the removal of the gills and gastrointestinal tract affect phase angle?

Removing the gills and gastrointestinal tract soon after capturing fish is commonly undertaken to preserve the seafood quality of species targeted in recreational and commercial fisheries (Haard 1993). Our results found that this practice significantly effects phase angle measurements taken along both the dorsal musculature and ventral tissue of kingfish. These findings indicate that phase angle measurements are only comparable within groups of individuals that have had gills and gastrointestinal tract removed, or within groups of intact

individuals. Whenever possible, we recommend taking phase angle measurements prior to the removal of the gills and gastrointestinal tract due to variability in the amount of tissue removed when fish are processed due to, for example, different techniques used by fish processors. Greater differences were found between before and after phase angle measurements taken along the ventral tissue of kingfish, which is the anatomic location associated with the greatest tissue loss when removing the gills and gastrointestinal tract, than for measurements taken along the dorsal musculature. This indicates that impedance measurements along the ventral tissue are most sensitive to the effects of gill and gastrointestinal removal, suggesting that phase angle should be measured along the dorsal musculature of fish that have undergone processing to best control for these effects.

4.5.3 - How does the anatomic location of measurement and fish size affect phase angle?

Consistent with previous studies showing that BIA measurements are specific to the anatomic location of electrode placement (Cox *et al.* 2011; Hafs and Hartman 2011), phase angle was significantly greater for measurements taken along the dorsal musculature than for measurements taken along the ventral tissue of kingfish. These differences are due to variation in the type of tissue present at dorsal and ventral locations and the ability of resistance and reactance measurements to differentiate between tissue types. The sensitivity of impedance measurements to varying tissue types (e.g. skeletal muscle, nervous tissue, kidney tissue, fat and bone) has been known for decades (Geddes and Baker 1967), and our results strengthen the body of evidence that demonstrates the need to control for anatomic location when deriving comparable biological body condition data (Cox and Heintz 2009; Cox *et al.* 2011; Hafs and Hartman 2011). Given that organs within the peritoneal cavity of fish undergo ontogenetic changes (e.g. due to growth and spawning) (Van Aerle *et al.* 2004), it is pragmatic to take

impedance measurements along the dorsal musculature of fish to minimise these effects on phase angle comparisons. Phase angle measurements taken along the dorsal musculature of kingfish were not affected by fish length or weight, suggesting that this location is most suitable for taking comparable phase angle measurements on fish of varying sizes.

4.5.4 - Can icing fish post-capture control for temperature effects on phase angle measurements?

The effect of temperature on impedance measurements (Buono *et al.* 2004; Cox *et al.* 2011; Hartman *et al.* 2011; Stolarski *et al.* 2014) may be the primary limitation to opportunistically applying BIA in the field, particularly for comparing the body condition of species that occupy broad thermal niches. For example, temperature was found to have a significant negative effect on resistance and reactance measurements taken on tailor (*Pomatomus saltatrix*) that were held at 15°C and 27°C (Hartman *et al.* 2011). Similarly, phase angle measurements in pink salmon (*Oncorhynchus gorbuscha*) were slightly effected over an 8°C temperature range (Cox and Heintz 2009). The influence of temperature on impedance measurements has prompted research into the developed of correction factors to account for variation in temperature when using BIA to predict proximate body condition indices, such as per cent dry mass (Hafs and Hartman 2015). However, it remains unclear if impendence measurements taken within relatively small temperature ranges (i.e. 1-2°C) are comparable (Cox and Hartman 2005) and if practical solutions, such as icing fish for short periods of time after capture, as suggested by Cox and Heintz (2009), can control for temperature effects. We found that phase angle measurements taken along the dorsal musculature of kingfish declined with temperature when repeated measurements were taken over approximately 20°C of temperature variation. Importantly, phase angle values were found to stabilise once the tissue

temperature of kingfish declined to approximately 5°C or after approximately 60 minutes of fish being held on ice. These findings support the notion that the effects of temperature on phase angle can be controlled by icing fish for a short period of time (e.g. 1 hour) post-capture (Cox and Heintz 2009), and highlight this as a practical solution to control for temperature effects (such as different water temperatures where fish were captured) during field-based sampling.

While our experiments highlight crucial considerations when developing protocols for the application of BIA to fish, the results are specific to kingfish and may not be transferable to other species due to the effects of variation in morphology and anatomic location of specific tissue types (Barlow 1961). In general, icing whole fish following capture and death, and taking dorsal measurements after 1 hour should lead to accurate and comparable data (Table 4.1). If this is not possible, researchers should examine potential biases using experiments that evaluate sources of variation for species of interest. Following the sampling protocol summarised in Table 4.1 will produce robust phase angle measurements that are (1) directly relevant to studies investigating *Seriola* spp., (2) relevant to studies applying BIA other medium- to large-bodied coastal-pelagic fishes, and (3) comparable with future studies that investigate other fishes.

4.5.5 - Additional considerations

Additional factors that were not experimentally investigated within this study may also influence phase angle measurements when opportunistically applying BIA in the field. Of particularly relevance to species caught in recreational and commercial fisheries is physiological stress associated with capture (Hartman *et al.* 2015), which varies depending on how fish are caught and killed. For example, the recreational capture of large pelagic fishes is

commonly associated with long angling durations (> 10 minutes) that can leave fish in poor condition once landed (Tracey *et al.* 2016). However, the advent of novel fishing technologies (e.g. automatic reels and line made from strong synthetic materials) means that fish can now be landed in shorter amounts of time and with less associated physiological stress. Thus, variation in physiological stress associated with angling duration may confound body condition comparisons using BIA. Similarly, fish that experience physiological stress associated with capture in certain gear types (e.g. gillnets) before being killed by a fisher may not be comparable with individuals caught using other methods (e.g. hook-and-line) and immediately killed. While philological stress associated with the method of fish capture may influence impedance measurements, no attempts have been made to quantify this potential effect. In the interim it is pragmatic to standardise the method of fish capture, where possible, to minimise variation in physiological stress and maximise the comparability of impedance data.

Variation in reproductive status has the potential to influence impedance measurements due to large fluctuations in gonad size and associated changes in relationship between lipid and moisture content during spawning periods (Domínguez-Petit *et al.* 2010; Jonsson *et al.* 1997). Despite this expectation, Stolarski *et al.* (2014) did not find an effect of reproductive status on impedance measurements taken on Dolly Varden (*Salvelinus malma*) despite gonads being on average 30 times larger (by weight) in spawning than in nonspawning individuals. These results suggest that detecting an effect of reproductive status on impedance measurements is dependent on whether electrical pathways intersect gonadal tissue, and highlight that this is not always the case even when measurements are taken along ventral tissue (Stolarski *et al.* 2014). Therefore, it may be possible to control for potential effects of reproductive status on impedance measurements by prioritising anatomic locations (e.g. dorsal musculature) that are likely to avoid the interaction of electrical currents with fish testes and ovaries. In the absence

of species-specific experiments, comparative body condition analyses using impedance data should aim to measure and control for reproductive status (e.g. categorising reproductive status and incorporating this variable into a mixed effects modelling framework). Regardless, BIA can handle variation in the spawning status of fish better than traditional morphometric-based condition indices as impedance measurements relate to the composition of fish tissue and are not influenced by the relationship between length and weight (Hartman et al., 2015).

Correction factors have been proposed to account for error arising from variation in factors that are known to affect BIA measurements (Cox et al., 2011; Stolarski et al., 2014; Hafs and Hartman, 2015). Temperature corrections have proven useful for reducing variability surrounding relationships between BIA measurements and laboratory-derived proximate composition indices (Stolarski et al., 2014; Hafs and Hartman, 2015). For example, Hafs and Hartman (2015) found that the application of temperature corrections to BIA models attempting to predict per cent dry mass reduced root-mean-squared error by an average of 32%. While correction factors are needed so that calibrated relationships between BIA measurements and proximate composition indices are useful in a variety of environmental contexts, developing these requires holding an adequate sample size of live individuals under experimental conditions. This is unlikely in situations where researchers do not have access to experimental facilities or when research projects are dependent on measurements taken on dead fish (e.g. Stolarski et al., 2014). In such cases, it is pragmatic to focus on measures that reflect relative physiological status (e.g. phase angle) rather than proximate composition, and to initially control for potentially confounding effects when taking measurements, rather than attempt to retrospectively correct for sources of error.

Understanding and controlling for factors associated with the handling of fish is crucial for the wide and robust application of BIA in fish and fisheries research. While studies have previously highlighted sources of error (Cox *et al.* 2011; Hafs and Hartman 2011), our results demonstrate the influence of factors that are specific to the opportunistic application of BIA to samples obtained from varied sources. It is in this context that BIA is particularly valuable due to the suitability of this approach for measuring the condition of species that are logistically difficult to sample using mass-based condition measures, and for quickly measuring the condition of a large number of individuals (e.g. commercial fisheries landings). By showing that factors likely to be encountered when applying BIA to samples from varied sources can confound impedance datasets, we encourage prospective BIA users to control for sources of variation so that comparable body condition data are available for ecological and fisheries management applications.

- Chapter 5 -

Oceanographic habitat suitability is positively correlated with the body condition of a coastal-pelagic fish [4]

5.1 - Abstract

Species distribution models are commonly used to determine a species' probability of occurrence but have not been used to examine the effect of environmental habitat suitability on fish condition, which is considered to be an integrated measure of physiological status. Here we test for a relationship between oceanographic habitat suitability and the body condition of kingfish (*Seriola lalandi*) from eastern Australia. We: (1) test if individuals sampled from areas of high-quality habitat were in better condition than individuals sampled from areas of low-quality habitat, and (2) assess if the condition of kingfish responded to oceanographic habitat suitability predicted at varying time-before-capture periods. Kingfish habitat was modelled as a function of sea surface temperature, sea level anomaly and eddy kinetic energy in a generalised additive modelling framework. Model projections were made over one- to six-week time-before-capture periods and compared to field-derived kingfish condition data measured using bioelectrical impedance analysis. Oceanographic habitat suitability was significantly correlated with kingfish condition at time-before-capture periods ranging from one to four weeks and became increasingly correlated at shorter lead-times. Our results highlight that: (1) fish condition can respond sensitively to environmental variability and this response can be detected using oceanographic habitat suitability models, and (2) climate change may drive extensions in species range limits through spatial shifts in oceanographic habitat quality that allow individuals to persist beyond historical range boundaries without their body condition being compromised.

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[4] **Chapter is published**: Champion, C., Hobday, A.J., Pecl, G.T., and Tracey, S.R. (2019) Oceanographic habitat suitability is positively correlated with the body condition of a coastal-pelagic fish. *Fisheries Oceanography*. https://doi.org/10.1111/fog.12457.

5.2 - Introduction

Species distribution or habitat suitability models have become valuable tools for assessing spatiotemporal variation in environmental habitat quality (Brodie *et al*., 2017; Hazen *et al*., 2018). These models have been successfully applied to predict the seasonal distributions of coastal-pelagic fishes (Brodie *et al.* 2015) and to identify shifts in their core (Dell *et al.* 2015; Hill *et al.* 2015) and range edge habitats under global change (Champion *et al.* 2018b; Robinson *et al.* 2015b). While projections created using habitat suitability models are commonly dependent on the probability of species occurrence (Robinson *et al.* 2011), these projections may also be used to provide novel insights into the physiological status of individuals across broad spatial extents. If physiological measures can be quantified, habitat models present a tool for testing the hypothesis that individuals from high-quality oceanographic habitat are in better condition than those from areas of low-quality habitat (Thorson 2015). Habitat suitability models are likely to prove valuable for this application because of their capacity to incorporate species' preferences for multiple environmental covariates (Waltari *et al.* 2014); meaning that an individual's condition can be simultaneously compared to the suite of variables that are known to be significant predictors of its habitat quality.

Species' physiological responses are predicted to vary with respect to the quality of their environmental habitats (Del Raye and Weng 2015). For example, concurrent reductions in reproduction, growth and feeding are expected to occur across a declining gradient of habitat suitability (Helaouët and Beaugrand 2009). While a range of measures have been applied to investigate environmental effects on the physiology of marine fishes, including moisture, ash, protein and lipids (Coleman *et al.* 2019), body condition indices are broadly considered to

represent an integrated measure of physiological status (Murphy *et al.* 1990). Although fish condition is known to covary with biotic factors, such as prey availability and spawning events (Cubillos and Claramunt 2009; Hiddink *et al.* 2016), environmental variation also affects fish either directly, due to physiological stress, or indirectly, through changes in ecosystem productivity (Lloret *et al.* 2014). Identifying relationships between environmental variables and species' physiology is particularly important for species of high conservation value or those targeted in fisheries as these can help explain variation between spawning stock biomass and subsequent recruitment (Morgan *et al.* 2011). For example, a positive correlation between body condition and bottom temperature for Atlantic cod (*Gadus morhua*) has been linked with variation in growth and recruitment among 10 spatially explicit stocks (Rätz and Lloret 2003). Similarly, sea surface temperature has been identified as an environmental predictor of body condition for multiple small pelagic species from the western Mediterranean and Gulf of Mexico (Adams *et al.* 2018; Brosset *et al.* 2015).

Current climate-driven changes to dynamic environmental variables may directly affect the condition of marine fishes. This is particularly relevant to coastal-pelagic fishes that display strong preferences for oceanographic habitats that are defined by combinations of environmental variables (Soberón and Nakamura 2009), such as temperature, current velocity and dissolved oxygen. Examples of climate-driven geographic shifts in the oceanographic habitats of coastal-pelagic fishes have been documented (Champion *et al.* 2018b; Hill *et al.* 2015), but how the condition of individuals throughout their distribution will respond to these changes remains unknown. For example, a species may be present in areas of both marginal and optimal habitat quality but the body condition of individuals from areas of marginal habitat quality may be relatively poor compared to individuals from areas of optimal habitat.

Investigating potential relationships between fish condition and oceanographic suitability presents an opportunity to address specific questions surrounding the effects of climate change on the spatial distribution of fishes, particularly at species range boundaries. For example, are individuals that extend beyond their historic range boundaries in poor condition due to the presence of suboptimal habitat suitability in novel environments? Applications for predictive relationships between fish condition and oceanographic habitat quality could also prove valuable for informing spatially dynamic conservation strategies (Howell *et al.* 2015). For example, management strategies that prioritise the protection of optimal oceanographic habitats for valuable species could be developed to conserve individuals in good condition and thus with high reproductive capacity, or to harvest high-value individuals while reducing discard rates. The spatiotemporal resolution of habitat suitability projections will ultimately limit the potential for making accurate comparisons with field-derived body condition measurements. Therefore, comparisons between habitat suitability projections and body condition measurements are currently most applicable to coastal-pelagic species with distributions correlated with remotely sensed oceanographic variables.

Assessments of the effects of environmental variables on fish condition have traditionally relied on condition indices, such as Fulton's K or relative weight (W_r), that are derived from measuring the deviation of individuals from expected length – weight relationships (Adams *et al.* 2018; Brosset *et al.* 2015). However, these condition estimates have been criticised as inaccurate and irrelevant to the likelihood of survival (Green 2001). One major issue is that most fishes are 60 – 90 % water and changes to this compositional component is likely to significantly affect measures of body condition that are based on total mass. For example, the tendency of fish to replace lipids with water when losing energy (Love 1970) is likely to mask any true reduction in body condition when using total mass-based estimates, like W_r (Hartman

and Margraf 2008). Other approaches for measuring proximate body composition parameters (e.g. per cent fat and per cent dry mass) are considered more accurate (Hartman and Margraf 2008) but require tissue sampling, usually requiring fish to be euthanased and substantial laboratory processing (Vogt *et al.* 2002) that is often expensive and time consuming.

Electrical conductivity methods have emerged as promising techniques capable of accurately estimating the proximate body condition of fishes in a fast and nonlethal manner (Hartman *et al.* 2015). Of these, bioelectrical impedance analysis (BIA) is a promising tool in fish and fisheries research because the instrument is portable and user-friendly (Cox and Hartman 2005), allowing measures of the electrical impedance of biological tissue under a wide range of field and laboratory conditions and fish sizes (Hartman *et al.* 2015; Willis and Hobday 2008). BIA works by passing a high frequency current (~50 kHz) of imperceptible amplitude (~800 μA) through body tissue between signal and receiver electrodes that are either pressed against the skin or inserted less than 1 cm into body tissue. The impedance of biological tissue to the electrical current can then be related to a suite of biologically relevant parameters or utilised as a high-resolution measure of relative fish condition (i.e. electrical phase angle). Subsequently, BIA is ideal for quickly (< 5 seconds) and non-lethally quantifying fish condition in the field (Willis and Hobday 2008) and could be widely used for assessing the effects of environmental habitat quality on fish physiology.

The objective of this study was to test for a relationship between oceanographic habitat suitability and the body condition of a coastal-pelagic fish species. Specifically, we aimed to: (1) test if individuals sampled from areas of high-quality habitat were in better condition than individuals sampled from areas of low-quality habitat, and (2) assess if the condition of kingfish responded to oceanographic habitat suitability predicted at varying time-before-

capture periods. By addressing these aims we seek to understand if dynamic oceanographic variables can serve as predictive covariates for the body condition of coastal-pelagic fishes, and to explore potential effects of climate change on the spatial distribution of individuals in good condition relative to those in poor condition.

5.3 - Methods

5.3.1 - Study species and extent

This study was undertaken in the coastal-pelagic environment adjacent to eastern Australia (Figure 5.1). The oceanography of this region is dominated by the poleward-flowing East Australian Current (EAC), which is strengthening due to increased wind stress over a broad region of the South Pacific associated with climate change (Cai *et al.* 2005; Sloyan and O'Kane 2015). Subsequently, south-eastern Australia's marine environment is among the most rapidly warming regions of the global ocean (Hobday and Pecl 2014). Diverse marine taxa have been documented responding to these oceanographic changes by undergoing poleward distribution shifts (Malcolm and Scott 2017; Ramos *et al.* 2015; Sunday *et al.* 2015). The rapid climate-driven physical and biogeographic changes occurring off south-eastern Australia presents a novel opportunity to investigate the influence of varying oceanographic habitat quality on the body condition of marine fishes throughout their distributions.

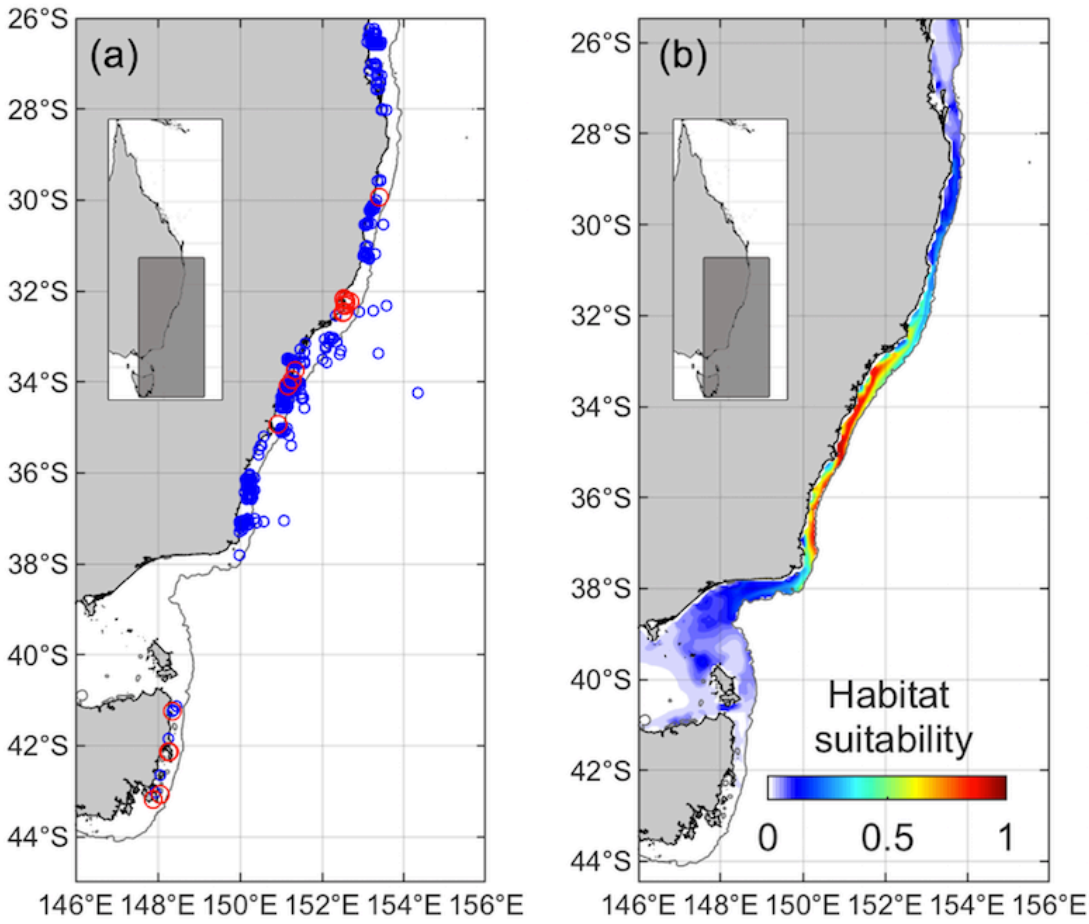

Figure 5.1. (a) Map of south-eastern Australia indicating the spatial distribution of kingfish occurrence records (blue circles; n = 1203) used to parametrise the habitat suitability model and the location of kingfish sampled for body condition data using bioelectrical impedance analysis (red circles; n = 113). (b) Example of a spatial projection of kingfish oceanographic habitat suitability nearshore of the continental shelf-break (i.e. where body condition sampling was undertaken) for the first week of January 2018. The grey line offshore of the coast represents the 200-m isobath.

The study species for this research was the yellowtail kingfish *Seriola lalandi* (hereafter 'kingfish'). Kingfish occur across coastal and pelagic environments (Gillanders *et al.* 2001) and individuals from south-eastern Australia are known to be from a single, genetically distinct population (Miller *et al.* 2011). Recent analyses have revealed that the distribution of oceanographic habitat for kingfish from eastern Australia has rapidly shifted poleward over the past 20 years (Champion *et al.* 2018b). These analyses are supported by photo-verified

observations of kingfish poleward of their historic southern Australian range boundary recorded by the Range Extension Database and Mapping Project (Redmap; www.redmap.org.au; Pecl *et al*., 2019b) and a rapid assessment of species that are likely to be undergoing poleward range extensions in south-eastern Australia (Robinson *et al.* 2015a). Taken together, these findings have provoked questions about potential relationships between oceanographic habitat quality and the relative body condition of kingfish throughout south-eastern Australia, including at their poleward range edge.

5.3.2 - Body condition: bioelectrical Impedance Analysis

The body condition of 113 kingfish from south-eastern Australia was measured between December and March over three consecutive austral summer-autumn periods (2016/17 – 2018/19) using bioelectrical impedance analysis (Figure 5.1a) in accordance with the sampling protocol developed in Chapter 4. Kingfish were sampled using hook-and-line fishing by the study authors and volunteer recreational fishers. Despite no evidence to suggest that body condition measurements were dependent on fish size (Figure 4.6), we restricted our analysis to juvenile kingfish only (confirmed through visual inspection of gonads) as the reproductive status of some mature fishes is known to influence their body condition (Lloret and Planes 2003; Millán 1999). Three replicate impedance measurements were taken along the dorsal musculature of individual kingfish held on ice for one hour post-capture on a nonconductive surface using the Seafood Analytics Certified Quality Reader (CQ Foods, Inc., Clinton Township, MI, USA). The mean of multiple measurements for each individual was calculated for subsequent analyses. Time-since-death has a negative effect on kingfish body condition, however, there is no significant difference in the bioelectrical impedance of fresh kingfish and kingfish that have been held on ice for up to 15 hours (Figure 4.5). Therefore,

body condition measurements for kingfish taken one-hour post capture, as done here, provide a repeatable measure of the body condition of wild kingfish.

Impedance is the sum of two vectors of electrical current, resistance and reactance, which are measured directly by the BIA tool. Resistance (R) measures the ability of extracellular material to conduct electricity (Cox and Hartman 2005) and subsequently reflects extracellular material, such as fat, which is nonconductive and can be indicated by higher measurements of R (Cox *et al.* 2011). Reactance (X_c) is the ability of a substance to hold a charge and is used in BIA to measure opposition of the cellular lipid bilayer to an alternating current (Cox *et al.* 2011). Subsequently, X_c is a measure of the total volume of healthy cells, which is relatable to an individual's body condition (Gabriel *et al.* 1996; Hartman *et al.* 2015). Measures of R and X_c were used to derive values of electrical phase angle (degrees), which is a metabolic condition index (Willis and Hobday 2008), of kingfish samples:

$$\text{phase angle } (^\circ) = \left(\arctan\left(\frac{X_c}{R}\right)\right) \times \frac{180^\circ}{\pi} \quad (1)$$

Phase angle is a specific measurement of the angle between the R (ohms) and X_c (ohms) vector components of impedance. Phase angle ranges from 0° to 90°, where higher values indicate good body condition due to high readings of X_c that are indicative of large quantities of intact cell membranes (Foster and Lukaski 1996). Unlike body composition measurements calculated using BIA (e.g. per cent fat), phase angle avoids the need to calibrate regression equations based on previous measurement of a representative sample (Cox and Hartman 2005). The use of phase angle instead of regression analysis for describing composition variables has become common in medical fields because phase angle is linked to metabolic rate and nutritional status, and can thus be used as a direct measure of body condition (Barbosa-Silva *et al.* 2003). This is

because phase angle measures the relationship between cell membrane potential and the distribution of intra- and extracellular water, which is correlated with metabolic turnover and is indicative of nutritional status (Barbosa-Silva *et al.* 2003). For example, a malnourished person and a highly trained athlete may share similar body compositions but have opposing metabolic rates (lower for malnourished people), which is an important difference among individuals that may appear to be in similar condition. In fish, electrical phase angle has been successfully used as a single predictor of body condition (Cox and Heintz 2009; Willis and Hobday 2008) and has been suggested as a useful measure for determining the quality of the habitat an individual has been sampled from (Cox and Heintz 2009). Here we quantify electrical phase angle from impedance measurements to compare the relative body condition of wild kingfish to the suitability of local oceanographic conditions for this species.

5.3.3 - Kingfish oceanographic habitat modelling

An oceanographic habitat model for kingfish from south-eastern Australia was developed to test for climate-driven shifts in the spatial distribution of preferred oceanographic conditions (Champion *et al.* 2018b). This model identified that sea surface temperature, sea level anomaly and eddy kinetic energy are significant environmental predictors of kingfish occurrence. Kingfish occurrence records (GPS locations) obtained from a recreational catch-and-release tagging program administered by the New South Wales Department of Primary Industries were used to parameterise this habitat model. Limitations associated with recreational fishery-dependent data, including spatiotemporal sampling biases and unreported fishing effort, constrain the utility of these data for directly inferring species distribution and abundance. Furthermore, species absence records are uncommon in fishery-dependent datasets, preventing the true probability of species occurrence to be modelled using these data

(Pearce and Boyce, 2006). Nevertheless, fishery-dependent species occurrence records are a valuable resource for modelling environmental habitat suitability due to the large number of data points and the broad geographic coverage common within these datasets (Brodie *et al*., 2015; Hill *et al*., 2016). Following data processing procedures undertaken to ensure spatial and temporal independence among tagging records (Champion *et al.* 2018b) and restricting the database from 1996–2017 to match the availability of satellite-derived environmental covariates, a total of 1203 kingfish occurrence records were available for analysis (Figure 5.1). These occurrence records were combined with 20,000 pseudo-absence points randomly generated throughout the study area to categorise unsuitable environmental habitat for kingfish, thus providing a binomial response variable for statistical modelling. Twenty thousand pseudo-absences were selected to: (1) ensure that environmental variability occurring over the spatiotemporal extent encompassed by the occurrence dataset was adequately captured, (2) comply with Barbet-Massin *et al.* (2012) who recommend selecting a large number (i.e. > 10,000) of pseudo-absences when using regression techniques to develop species distribution models, and (3) facilitate comparisons with habitat suitability models for other pelagic fishes from eastern Australia that were also developed using approximately 20,000 pseudo-absences (e.g. Brodie *et al.* (2015) and Hill *et al.* (2016) who used 20,000 and 23,242 pseudo-absences, respectively). Explanatory oceanographic variables were matched to the resulting set of occurrence and pseudo-absence data using the Spatial Dynamics Ocean Data Explorer (Hartog *et al.* 2011a). Oceanographic variables were initially selected based on their likely importance to coastal-pelagic fishes (Hobday and Hartog, 2014), prior knowledge of variable collinearity and spatiotemporal coverage of the study domain. For example, satellite-based chlorophyll estimates are significantly correlated with sea surface temperature in this region and have incomplete spatial and temporal coverage so were not included in model selection. Following initial screening, sea surface temperature (SST), sea level anomaly (SLA), dissolved oxygen

(DO) and eddy kinetic energy (EKE) were included in a formal model procedure (see Table 2.1 in Chapter 2 for a full description of oceanographic products utilised). However, a strong correlation between SST and DO (r = -0.77) resulted in the retention of SST and removal of DO from the suite of explanatory variables because collinearity among predictor variables generally has a negative effect on model performance (Zuur *et al.* 2007).

Kingfish oceanographic habitat suitability was described using a generalised additive mixed model (GAMM), applying the logistic link function to relate the binomially distributed response variable (i.e. kingfish occurrence or pseudo-absence) to oceanographic predictors. Because fishing effort information was not available in the tagging database, calendar year was included as a random effect to account for inter-annual variability in catch-per-unit effort. A forward model selection procedure and k-fold cross-validation process was utilised to determine the most parsimonious GAMM, which has the form (in script notation):

$$Response = s(\mathrm{SST}) + \mathrm{SLA} + s(\mathrm{EKE}) + (1|\mathrm{Year}) \qquad (2)$$

where *Response* is the oceanographic habitat suitability for kingfish (scaled between 0 and 1) modelled as a function of SST, SLA and EKE, with Year included as a random term. Penalised regression spline-type smoothers of moderate rank are denoted by s. A full description of the model selection and evaluation procedures used to specify this habitat suitability model and identify that it has good predictive skill (i.e. mean AUC = 0.887 ± 0.002 SD) are presented in Chapter 2. Furthermore, the partial effects of each predictor variable on kingfish occurrence are presented and discussed in Chapter 2.

5.3.4 - Comparison of kingfish oceanographic suitability and body condition

Daily oceanographic suitability values were extracted from model projections (e.g. Figure 5.1b) over one- to six-week time-before-capture periods for all locations that kingfish were sampled for body condition measurements (Figure 5.2). The spatial resolution of kingfish habitat projections was dependent on the largest common resolution of the oceanographic covariates, and as a result all projections of kingfish oceanographic habitat were resolved to 0.1°.

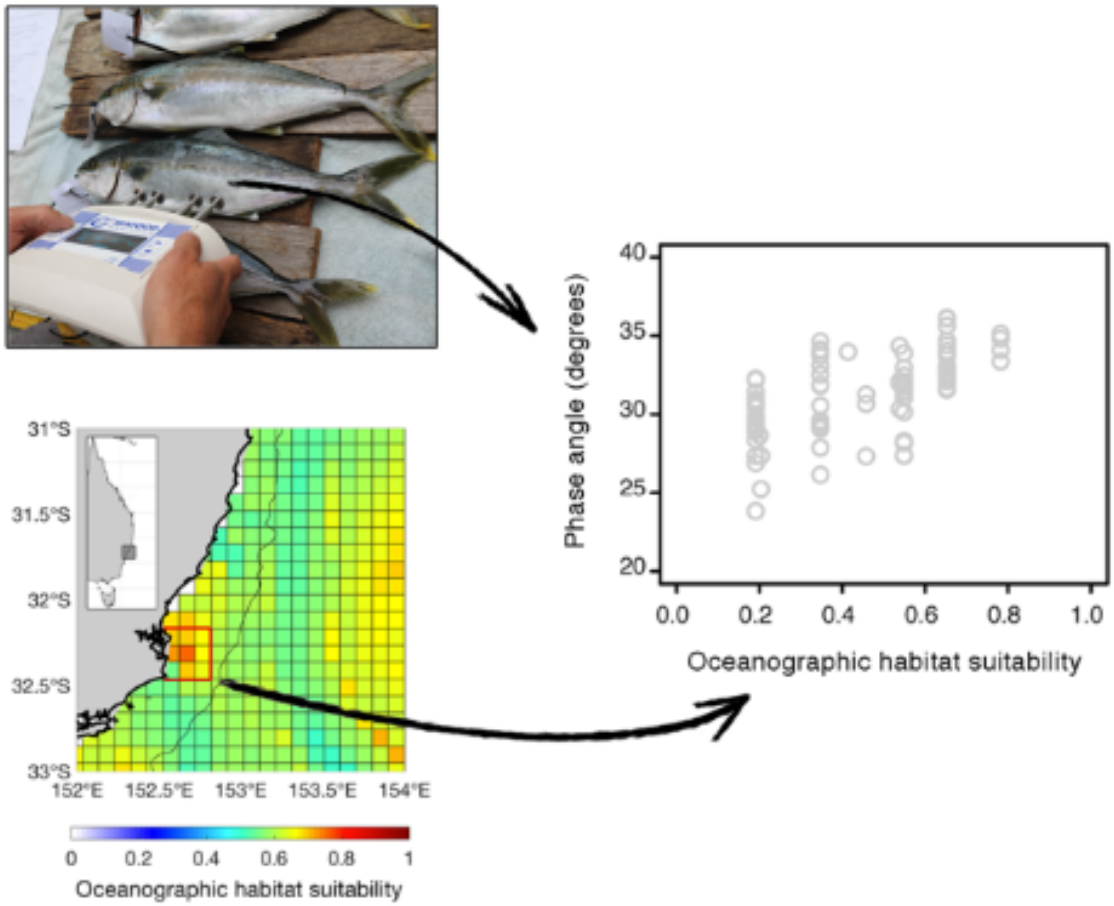

Figure 5.2. Bioelectrical impedance analysis (in use in photograph at top-left) and spatial predications of kingfish oceanographic habitat suitability (figure at bottom-left) we combined to assess for a relationship between habitat quality and the body condition of kingfish (*Seriola lalandi*) from south-eastern Australia (right; subset of real data presented in this chapter).

Daily habitat suitability values surrounding fish capture locations were averaged to create single estimates for 1, 2, 3, 4, 5 and 6 weeks prior to the date of fish capture, allowing for comparisons between habitat suitability and kingfish condition at varying time-before-capture periods. Because coastal-pelagic fishes are unlikely to entirely associate with the location of fish capture over the preceding 6-week period, oceanographic habitat projections created at longer time-before-capture periods (i.e. 5 – 6 weeks) encompassed a greater area of habitat surrounding fish capture locations than habitat projections created over shorter (i.e. 1 – 2 weeks) lead-times. The kingfish tag-recapture database (used to parameterise the habitat model described above) also contained 646 straight line distances between fish tagging and recapture locations. These data were used to estimate the area of oceanographic habitat to include in comparisons with body condition data over different lead-times as no electronic tagging data were available for more accurate movement estimates. Straight line distances between kingfish captures were compared over a period ranging from 0 to 6 weeks at liberty, with the line of best fit for these data used to determine the area of oceanographic habitat to include for different time-before-capture periods investigated. Given the difficulty of estimating the area of oceanographic habitat that is likely to encompass the location of kingfish over longer (i.e. 3 – 6 weeks) time-before capture periods, we also applied 70^{th}, 80^{th} and 90^{th} percentile fits to the tag-recapture data, which represent increasingly broader areas of oceanographic habitat surrounding kingfish sampling locations. This allowed for exploration of the relationship between fish condition and oceanographic habitat quality over varying time-before-capture intervals while accounting for the uncertainty surrounding the recent location of kingfish relative to the location of capture.

Linear models were used to assess for relationships between oceanographic habitat suitability surrounding locations of fish captures on the body condition of kingfish measured using BIA.

Individual models were fitted to data representing oceanographic conditions at 1-, 2-, 3-, 4-, 5- and 6-week time-before-capture periods. Where significant relationships between kingfish condition and oceanographic habitat suitability were identified, the variation in kingfish body condition explained by oceanographic habitat suitability in each model was examined using r^2 values. Model residuals were compared with additional factors, including latitude of fish capture and fish size (Figure 5.3 and 5.4, respectively), to determine if the linear models could benefit from the addition of random effects to account for potential intra-class correlations. However, the residuals from linear models did not show any clear patterns when plotted against additional factors so no random effects were included (Zuur *et al*. 2013).

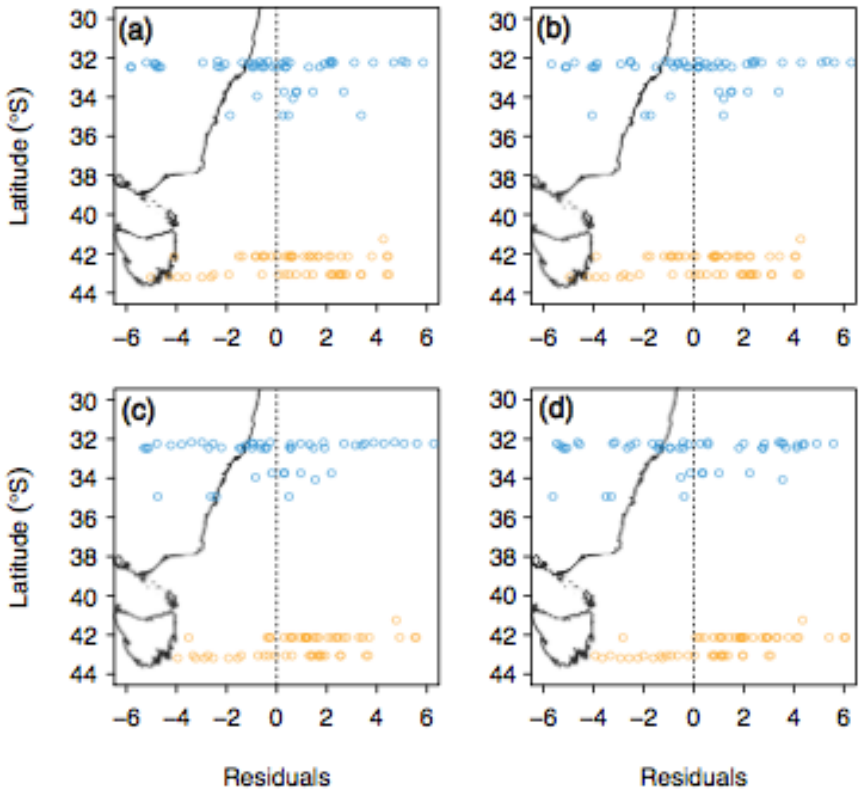

Figure 5.3. Distribution of residuals (method: line of best fit presented in Figure 5.6) from linear models fitted to kingfish body condition data and oceanographic habitat suitability predicted at time-before-capture periods of (a) one, (b) two, (c) three, and (d) four weeks across the latitudinal extent of this study. Generally, model residuals are evenly distributed around 0 throughout the spatial extent of this study, indicating that the models fitted field data from Tasmania (orange data points) and NSW (blue data points) similarly.

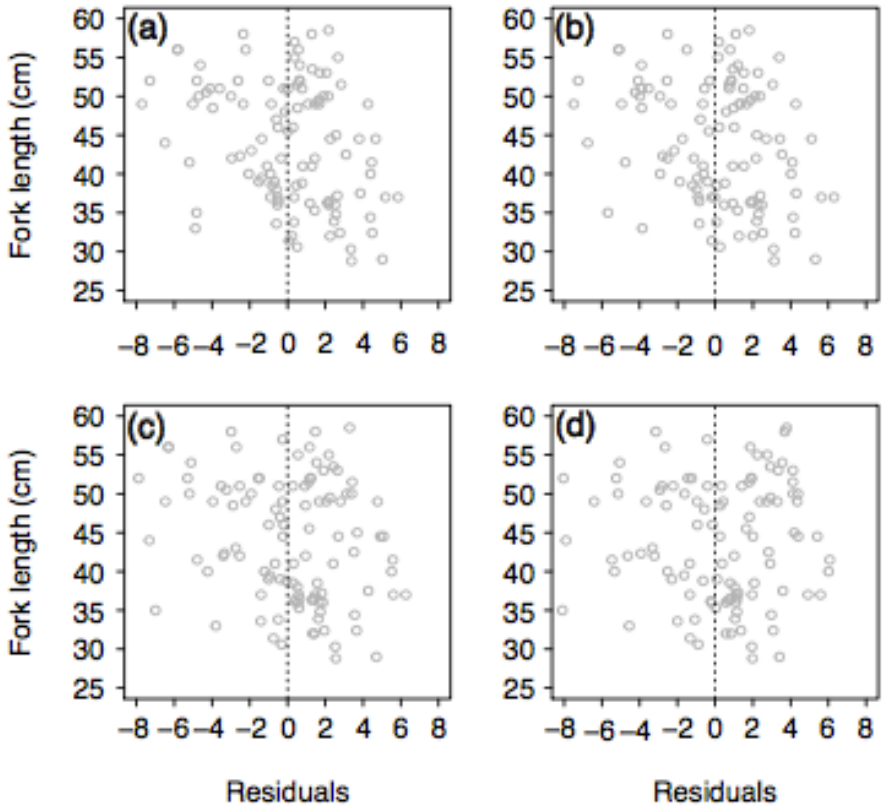

Figure 5.4 Distribution of residuals (method: line of best fit presented in Figure 5.6) from linear models fitted to kingfish body condition data for juvenile kingfish of varying sizes and oceanographic habitat suitability predicted at time-before-capture periods of (a) one, (b) two, (c) three, and (d) four weeks. Model residuals are evenly distributed around 0 for kingfish of varying sizes, indicating that the relationship between habitat suitability and fish condition was consistent between different sized individuals.

Diagnostic plots were visualised for each linear model fitted to assess if the assumptions of normality and homogeneity of variance were satisfied. Statistical analyses were undertaken using the R programming language (R Core Team 2017). GAMMs were fitted using the 'gamm4' package (Wood and Scheipl 2013). Daily oceanographic habitat projections were compiled in Matlab (ver. 9.2, The MathWorks, Inc., Natick, MA, USA). Kingfish were sampled in accordance with the University of Tasmania's Animal Care and Ethics approval number A0016150.

5.4 - Results

Kingfish sampled from areas of relatively high oceanographic habitat quality were generally in better condition than individuals sampled from areas of lower quality habitat (Figure 5.5). Specifically, the body condition of kingfish was significantly correlated with oceanographic habitat suitability at time-scales up to four weeks prior to fish capture (Figure 5.6), predicted over the spatial extent corresponding to average kingfish movements in south-eastern Australia (Figure 5.7a). The strength of the relationship between kingfish condition and habitat suitability was similar when habitat projections incorporated oceanographic data from one and two weeks prior to capture ($F_{1, 111} = 59.79$, $P < 0.001$; $r^2 = 0.35$ and $F_{1, 111} = 61.48$, $P < 0.001$; $r^2 = 0.36$, respectively), and became progressively weaker when incorporating oceanographic data from three ($F_{1, 111} = 38.99$, $P < 0.001$; $r^2 = 0.26$) and four ($F_{1, 111} = 26.75$, $P < 0.001$; $r^2 = 0.16$) weeks prior over an increasing spatial extent (Figure 5.6). Relationships were non-significant at time-scales greater than four weeks prior to capture.

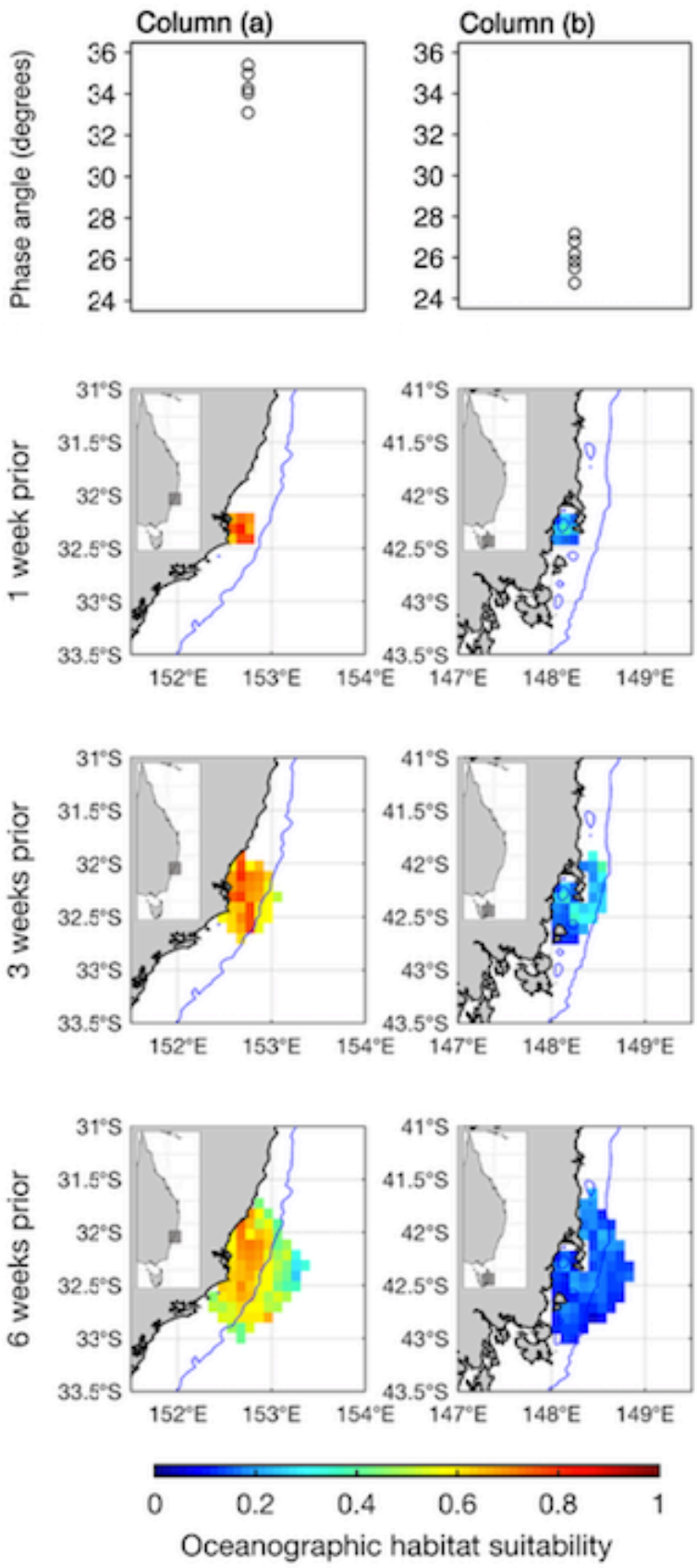

Figure 5.5. A subset of kingfish sampled from south-eastern Australia in relatively good condition (column a; n = 5) that were sampled on 18 January 2018 from an area of oceanographic habitat quality that remained highly suitable over the preceding 1-, 3-, and 6-week time-before-capture periods, and relatively poor condition (column b; n = 6) sampled on 20 February 2019 from an area of oceanographic habitat quality that remained comparably less suitable over the preceding 1-, 3-, and 6-week time-before-capture periods. Habitat suitability averages corresponding to 1-, 3-, and 6-week time-before-capture periods were calculated using 8.5, 25.5 and 51 km straight line distances from locations of fish capture, respectively. The blue line represents the 200-m isobath. NB: Although examples in columns (a) and (b) are from different latitudes, kingfish body condition did not display a latitudinal trend but varied with respect to the dynamic oceanographic variables that determine suitable environmental habitat for this species.

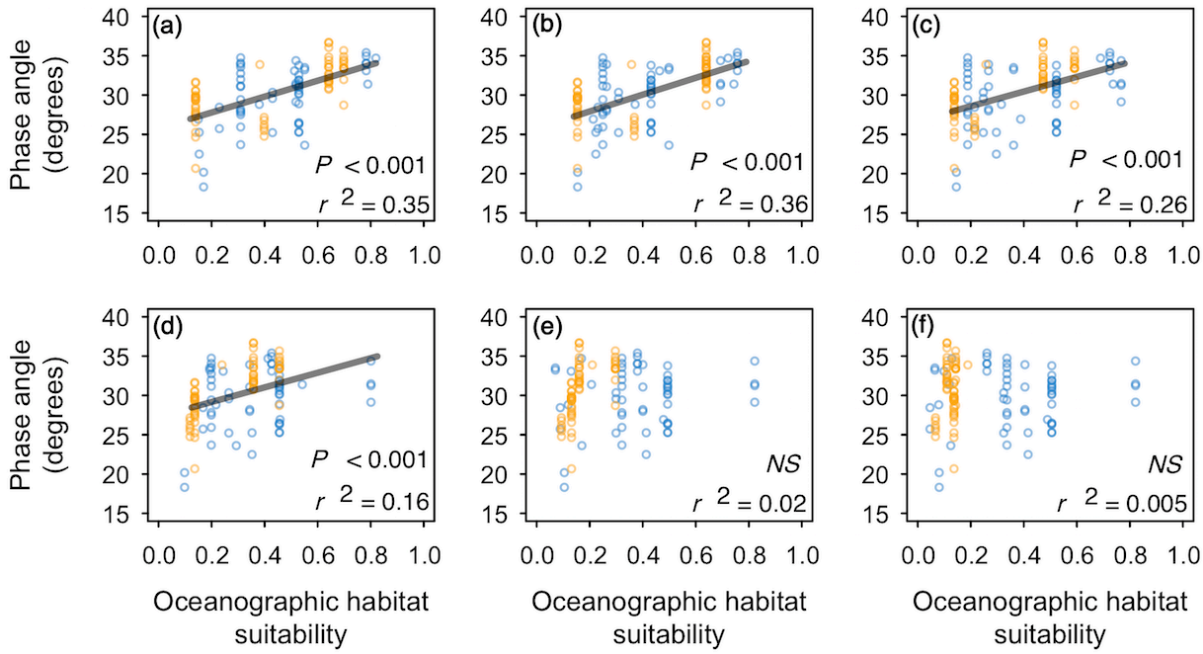

Figure 5.6. Relationships between kingfish body condition measured using bioelectrical impedance analysis (phase angle) and oceanographic habitat suitability predicted at time-before-capture periods of (a) one, (b) two, (c) three, (d) four, (e) five, and (f) six weeks. Blue and orange data points denote samples from NSW and Tasmanian coastal waters, respectively. *NS* denotes non-significance. Data presented in this figure are based on habitat suitability projections that vary spatially according to the line of best fit applied to movements of kingfish over a six-week period derived from a large tag-recapture database (n = 646; Figure 5.7a).

The strongest relationship between kingfish condition and oceanographic habitat suitability was found when the area of spatial habitat included in analyses was defined by the linear line of best fit applied to tag-recapture data, and became progressively weaker when increased spatial habitat was included in comparisons based on 70th, 80th and 90th percentile regression fits (Figure 5.7b). Results of comparative analyses between kingfish body condition and oceanographic habitat suitability that used 70th, 80th and 90th percentile fits to include a greater area of oceanographic habitat for comparison with body condition measurements are presented in Table 5.1.

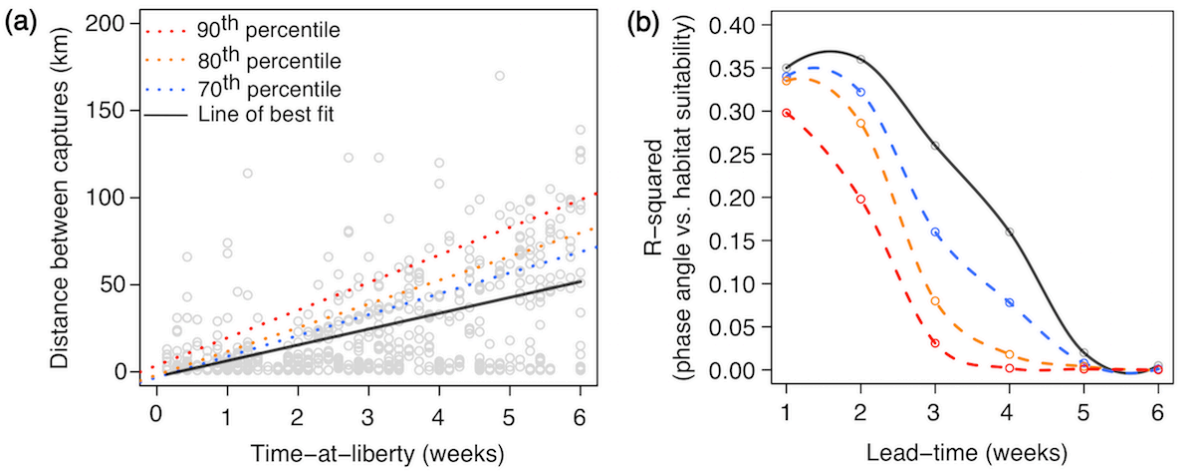

Figure 5.7. (a) Percentile regression fits for kingfish tag-recapture data and (b) the resulting correlation between kingfish body condition measurements and oceanographic habitat suitability projections at varying time-before-capture periods calculated over spatial scales corresponding to the percentile regression fits in plot (a). The solid line in plot (b) shows the relationship between kingfish condition and habitat suitability assuming that the movements of kingfish sampled for body condition measurements approximate the median of all fish recorded in the tag-recapture database (data presented in plot (a)). Habitat projections based on the 90th percentile fit (dashed red lines) incorporate the broadest area of oceanographic habitat surrounding locations of fish sampled for body condition measurements, providing a conservative estimate of the relationship between kingfish condition and habitat suitability at varying time-before-capture periods.

Table 5.1. Summary statistics for all linear models fitted to comparisons between kingfish oceanographic habitat suitability and body condition. r^2 values for all comparisons are presented in Figure 5.7b.

Spatial and temporal extent of oceanographic habitat included in comparisons with kingfish body condition, derived from tag-recapture data (n = 646)		kingfish body condition *vs*. habitat suitability		
Method: Line of best fit (black line Figure 5.7)	Straight line distance determining habitat area (km)	$F_{1, 111}$	P	r^2
1-week time-before-capture period	8.5	59.89	< 0.001	0.358
2-week time-before-capture period	17	61.48	< 0.001	0.361
3-week time-before-capture period	25.5	38.99	< 0.001	0.255
4-week time-before-capture period	34	26.75	< 0.001	0.157
5-week time-before-capture period	42.5	3.23	0.075	0.024
6-week time-before-capture period	51	2.66	0.106	0.005
Method: 70th percentile fit (blue dashed line Figure 5.7)				
1-week time-before-capture period	10.7	59.12	< 0.001	0.340
2-week time-before-capture period	21.4	56.23	< 0.001	0.322
3-week time-before-capture period	32.1	22.11	< 0.001	0.161
4-week time-before-capture period	42.8	8.10	0.005	0.078
5-week time-before-capture period	53.5	2.37	0.127	0.008
6-week time-before-capture period	64.2	1.66	0.201	0.001
Method: 80th percentile fit (orange dashed line Figure 5.7)				
1-week time-before-capture period	13.1	59.08	< 0.001	0.335
2-week time-before-capture period	26.2	55.71	< 0.001	0.286
3-week time-before-capture period	39.3	13.36	< 0.001	0.080
4-week time-before-capture period	52.5	4.11	0.045	0.018
5-week time-before-capture period	65.5	1.63	0.204	0.004
6-week time-before-capture period	78.6	1.22	0.272	0.001
Method: 90th percentile fit (red dashed line Figure 5.7)				
1-week time-before-capture period	16.6	52.67	< 0.001	0.298
2-week time-before-capture period	33.2	47.02	< 0.001	0.198
3-week time-before-capture period	49.8	7.89	0.006	0.031
4-week time-before-capture period	66.4	3.99	0.048	0.002
5-week time-before-capture period	83	1.29	0.258	0.001
6-week time-before-capture period	99.6	1.14	0.288	0.001

5.5 - Discussion

Comparing body condition data measured using bioelectrical impedance analysis and modelled oceanographic suitability revealed a significant positive relationship between the physiological status of kingfish and the quality of recently occupied environmental habitat. These findings are consistent with previous research that has demonstrated links between environmental variation and fish condition (Adams *et al.* 2018; Brosset *et al.* 2015; Lloret *et*

al. 2014; Oliva-Paterna *et al.* 2003). However, this study is unique in that body condition data were compared to oceanographic habitat suitability that was determined by multiple dynamic environmental variables. The strength of this relationship was comparable for comparisons at 1- and 2-week time-before-capture periods and deteriorated as kingfish body condition data were compared to habitat projections that incorporated longer lead-times and increasing spatial extents. This trend highlights the spatiotemporal dynamics of the oceanographic variables that are significant predictors of the distribution of kingfish from eastern Australia (Brodie *et al.* 2015; Champion *et al.* 2018b). For example, mesoscale oceanographic features in this region vary over temporal scales ranging from hours to months (Suthers *et al.* 2011). Nevertheless, statistically significant relationships between kingfish condition and oceanographic habitat quality were identified out to four weeks prior to capture. This temporal range is comparable with the predictive skill of a temperature-based habitat forecast developed for bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight, which provided useful projections of the species' distribution up to two months ahead of time (Eveson *et al.* 2015). While studies have focused on forecasting species occurrence (Brodie *et al.* 2017; Eveson *et al.* 2015), comparisons among relationships between fish condition and the oceanography prior to capture remain limited by a paucity of empirical data.

The persistence of suitable oceanographic conditions for kingfish off eastern Australia during Austral summer and autumn periods (Brodie *et al.* 2015) is likely to underpin our ability to detect the influence of environmental habitat on fish condition at time-before-capture periods of approximately one month. Specifically, 49% of body condition against habitat quality comparisons were made over three consecutive summer/autumn periods off eastern Australia when the temporal persistence of high-quality habitat for kingfish is greatest (Champion *et al.* 2019b). This is primarily driven by the partial effect of SST on our kingfish habitat model,

which produces positive habitat suitability estimates when values between ~18°C and ~25°C (peaking at 22°C) are used in projections. As a result, oceanographic habitat quality for kingfish off eastern Australia during summer and autumn, when SST ranges from ~19°C to ~24°C, remained consistent in this region over the range of time-before-capture periods investigated. In contrast, kingfish habitat quality is temporally variable off eastern Tasmania during the austral summer and autumn (Champion *et al.* 2019b) primarily due to the persistence of marginally suitable SST during this period. This is evident in the greater relative change in habitat suitability values for eastern Tasmania (orange data points, Figure 5.6) than for eastern mainland Australia (blue data points, Figure 5.6) over the range of time-before-capture periods that we investigated. Therefore, incorporating data from the Tasmanian coastal ocean subsequently reduced the maximum time-before-capture period that a statistically significant relationship between habitat suitability and kingfish condition could be detected. Although SLA and EKE are also significant predictors of kingfish oceanographic habitat (Brodie *et al*., 2015; Champion *et al*., 2018), the relationship between these variables and temporal trends in the persistence of suitable kingfish habitat is less clear than for SST. Specifically, SLA has a positive linear effect on kingfish habitat suitability, indicating that kingfish occurrence is likely to be higher in convergence areas, while low EKE values have a positive effect on model parameters that declines at values greater than ~0.11 m^2 s^{-2}. Taken together, these findings suggest that kingfish found closer to their poleward range edge (i.e. coastal Tasmania) are likely to vary their habitat use over shorter time-scales than individuals from the core distribution (i.e. eastern mainland Australia) to avoid situations where oceanographic suitability rapidly declines and negatively affects body condition.

The relationship between kingfish body condition and spatiotemporally variable habitat quality provides a physiological explanation of the highly seasonal occurrence and poleward extension

of this species' range edge in Tasmania's coastal ocean (Champion *et al.* 2018b). Kingfish in this region may follow the annual poleward advance and equatorward retreat of suitable oceanographic habitat due to the direct effects of changing environmental conditions on their physiology or due to indirect effects on, for example, foraging success and spawning status. Longer term climate-driven changes to the spatial distribution of dynamic environmental habitats (Hill *et al.* 2015; Hobday 2010; Robinson *et al.* 2015b) may affect the body condition of redistributed species. For example, our results indicate that future oceanographic conditions predicted for eastern Australia (Hobday and Lough 2011) are likely to support the persistence of kingfish in high quality condition at higher latitudes. Given that fecundity is known to covary with body condition (Rätz and Lloret 2003), changes to the distribution of fish in 'good' condition due to climate-driven environmental change may aid the establishment of spawning populations in novel environments (Ling *et al.* 2009). The establishment of reproductive populations is a crucial step in the range extension pathway (Bates *et al.* 2014) and the spatial redistribution of individuals with relatively high reproductive output would expedite this process. Future research to improve our understanding of the relationship between global change and the distribution of highly fecund individuals is required to enhance our capacity to explain future variation in recruitment (Marshall and Frank 1999), and the progression of range extending species from early arrival stages to self-sustaining populations (Bates *et al.* 2014). Importantly, inferring the establishment of range extending species based on relationships between body condition and fecundity necessitates the prioritisation of sampling effort to ensure body condition data are measured at comparable phenological stages, such as non-spawning periods.

Our results indicate that habitat suitability models have the potential to describe substantial variation in fish body condition at a population level. Therefore, habitat models with good

predictive skill appear useful for not only identifying locations where a species is likely to be present or absent (Maxwell *et al.* 2009) but also for spatially differentiating between individuals in relatively good or poor body condition. These findings highlight that the relative body condition of a species throughout its distribution can be a more sensitive response to environmental variation than binary presence/absence data. For example, kingfish in this study were present in locations where habitat suitability was approximately equal to 0.1, however these individuals were found to be in relatively poorer condition than individuals sampled from locations where suitability values ranged from 0.6 to 0.8. Projections of habitat quality for locations where suitability values exceed the occurrence threshold could therefore be a novel method for investigating the physiology and ecology of other species that associate with oceanographic features. For example, in the development of a habitat suitability model for black marlin (*Istiompax indica*) in the Tasman Sea, Hill *et al.* (2015) identified a threshold value of 0.282 to partition between habitat that was suitable and unsuitable for the occurrence of this species. Spatial variability in habitat suitability values above such thresholds could serve as a proxy for physiology or ecological responses but further comparisons between field data and model projections are required to test these relationships. Ultimately, undertaking such comparisons in marine systems necessitates environmental datasets that are of a temporal resolution (i.e. daily to weekly) capable of accurately capturing the dynamic oceanographic process that influence species physiology and ecology.

The results of this study identify the potential to predict the relative body condition of kingfish from eastern Australia based on oceanographic conditions over the preceding four-week period within a radius of approximately 40 km of the location of capture. Given that fisher knowledge is known to correlate with projections from habitat suitability models (Mason *et al.* 2019), anglers identifying and fishing in optimal oceanographic conditions for kingfish are likely to

be catching fish in better condition relative to anglers fishing in suboptimal oceanographic habitat. Therefore, oceanographic habitat suitability projections for kingfish would be of value to fishers who aim to target the highest quality fish possible for the purpose of consumption, and who are willing to modify their behaviour to achieve this goal. Comparisons between phase angle measurements used to assess fish condition herein and various metrics for quantifying seafood quality (Coleman *et al.* 2019) could be undertaken to determine if the range of variation in phase angle measurements corresponds to meaningful changes in kingfish seafood quality. This is a necessary step before links are drawn between oceanographic habitat suitability and the spatial distribution of kingfish seafood quality off eastern Australia and subsequent implications (e.g. market value of kingfish) are discussed. It is more likely that relationships between seafood quality and environmental habitat suitability would be found for coastal-pelagic species that associate with dynamic oceanographic features, such as kingfish, than for estuarine species that have evolved broad physiological tolerances to environmental conditions. For example, Coleman *et al.* (2019) found that the seafood quality of a common sparid, yellowfin bream (*Acanthopagrus australis*), was not affected by experimental treatments simulating future climate change scenarios. Coleman *et al.* (2019) attributed the lack of a physiological responses in this species to its evolution in estuarine habitats that are characterised by high abiotic variability. In contrast, strong relationships between the distributions and ecologies of coastal-pelagic species and environmental variables have been documented (Briscoe *et al.* 2016; Brodie *et al.* 2015; Dell *et al.* 2011; Hobday 2010; Robinson *et al.* 2015b), indicating that environmental effects on the seafood quality of these species may be detectable.

Ecological interactions such as predator-prey relationships almost certainly influence the distribution and condition of marine species (Boyce and McDonald 1999). This is likely to be

true for kingfish from south-eastern Australia given that our results show oceanographic habitat suitability alone, assessed over a 2-week time-before-capture period, explained approximately 35% of variation in fish condition. Ecological interactions may be synergistic or antagonistic to the direction of the relationship between kingfish condition and oceanographic habitat suitability that we identified. For example, mismatches in oceanographic habitat preferences for kingfish and key prey species such as yellowtail scad (*Trachurus novaezelandiae*) and blue mackerel (*Scomber australasicus*) may result in good condition kingfish occurring in suboptimal oceanographic habitats. Incorporating interactions through the development of multi-species distribution models (Hui *et al.* 2015) has the potential to resolve the relative effects of environmental and ecological factors (Robinson *et al.* 2011) on species distributions. Expanding habitat models to incorporate biotic interactions is likely to be a valuable step towards enhancing our capacity to further explain variation in a species' body condition throughout its distribution.

- Chapter 6 – General discussion –

This thesis highlights the utility of species-environment relationships for assessing the effects of climate change on species distributions (Chapters 2 and 3), and for investigating how physiological responses are related to environmental heterogeneity (Chapter 5). Overarchingly, the results of this thesis demonstrate that species' responses to environmental conditions are crucial determinants of their distributions and physiological status and that a correlative understanding of these relationships is advantageous for detecting and adapting to the biological effects of global climate change.

6.1 Climate-driven redistribution of pelagic fishes

This thesis contributes to the current understanding of climate-driven species redistributions in marine systems, particularly for pelagic fishes. The average rate of species redistribution in marine systems has been reported as approximately 31 km decade^{-1} when analyses include both the trailing and leading edge of species distributions (n = 360 observations) and 72 km decade^{-1} when analyses include only the leading edge of species distributions (n = 111 observations) (Poloczanska *et al.* 2013). However, coastal-pelagic fishes are known to be responding more rapidly than this average (Hill *et al.* 2015), which has been attributed to traits of high adult mobility and broad latitudinal range size (Sunday *et al.* 2015). Results from Chapter 2 support a growing body of evidence demonstrating rapid climate-driven shifts in species that associate with dynamic oceanographic variables (Hazen *et al.* 2013). For example, core oceanographic habitat for kingfish from south-eastern Australia was found to have shifted poleward at a rate of 94.4 km decade^{-1} in response to climate-driven changes in regional oceanography between 1996 and 2015. Even more rapid spatial changes in the historical poleward range edge for kingfish were also identified, with results demonstrating

that a poleward extension has occurred at a rate of 108.8 km decade^{-1} over this period. The velocity of this poleward shift is notably faster than historical rates of range change identified for a suite of nearshore fishes using observational data (average rate of range change = 38 km decade^{-1}; Sunday *et al*., 2015) and for a mobile apex predator using habitat suitability projections (88.2 km decade^{-1}; Hill *et al*., 2015) from eastern Australia. These findings also markedly exceed future rates of poleward range shifts predicated for 16 commercially important offshore pelagic species from Australia by the year 2100 (average rate of range change = 40 km decade^{-1}; Hobday 2010).

Comparisons among rates of climate-driven range change should be interpreted cautiously due to the effects of varying data sources and methodologies that are used (Brown *et al.* 2016). For example, the results of Chapter 2 are based on projections of oceanographic habitat suitability determined from kingfish occurrences, which are known to produce faster range shift estimates than abundance-based measures that better reflect whole populations (Brown *et al.* 2016). Crucially, historical rates of change that utilise relationships between species and observed environmental variables (e.g. satellite-derived sea surface temperature) are not necessarily comparable with future projections that commonly rely on regionally downscaled global circulation model output to estimate future distributions (Chapter 3). Furthermore, the length of future projections (e.g. from the present to 2060, 2080, 2100 etc.), combined with variation in the baseline period averaged over to determine a species 'historical distribution', presents additional factors that can confound comparisons among rates of species redistribution. These biases challenge global comparisons of species range shifts (e.g. Parmesan and Yohe 2003; Poloczanska *et al.* 2013) and require greater recognition in the next iteration of global meta analyses of climate-driven species redistribution. Nevertheless, convergent lines of evidence, including Chapter 2 herein, indicate that marine species that associate with dynamic

oceanographic variables (e.g. zooplankton, pelagic fishes) are likely to most rapidly respond to the effects of climate change through shifts in distribution (Dell *et al.* 2011; Hill *et al.* 2015; Hobday 2010; Robinson *et al.* 2015b). This growing evidence-base suggests that coastal-pelagic fishes are well-suited for the development of science-based climate adaptation initiatives as the variables that correlate with their distributions are routinely sensed by satellites and are the focus of future oceanographic forecasts (Payne *et al.* 2017).

Predicting the future distributions of pelagic species is critical for dynamic seasonal forecasting (Hobday *et al.* 2011b) and bycatch mitigation (Hazen *et al.* 2018; Howell *et al.* 2008) in the short-term (i.e. weeks to months) and climate change adaptation in the mid- (i.e. years to decades) to long-term (i.e. decades to centuries) (Chapter 3). In all instances, future projections of species distributions should consider the information needs of user groups that can benefit from them. Important considerations include the lead-time of projections to ensure these align with human decision-making and/or political timescales and the delivery of future projections to ensure these are easily interpretable and relevant to stakeholders (Hobday *et al.* 2013). In the context of climate-driven species redistribution, this thesis identifies the temporal persistence of suitable environmental habitat, or the duration that preferred environmental conditions are sustained in particular regions, as a relevant metric for adaptation that is easily communicable (Chapter 3). Shifts in temporal persistence of species' environmental habitats remain an underappreciated aspect of climate-driven species redistributions (Champion *et al.* 2018b), and one that has tangible implications for stakeholders. Specifically, the duration of environmental habitat persistence in spatially explicit domains links to ecological, social and economic outcomes. For example, changes in the temporal persistence of suitable habitats for valuable or iconic species may equate to shifts in commercial and recreational fishing opportunity.

The results of Chapter 3 demonstrate spatial variation in the future effects of climate-driven oceanographic change on the temporal persistence of kingfish habitat throughout south-eastern Australia. This information is directly relevant to climate change adaptation by fishers and managers of this resource. For example, when faced with reduced fishing opportunity due to declining habitat persistence (e.g. in the Tweed-Morton bioregion presented in Chapter 3), recreational anglers may adapt by travelling to fish different locations, fishing for longer each season or targeting different species (van Putten *et al.* 2017). Similarly, when fishing opportunity increases (e.g. in the Batemans Shelf, Twofold Shelf and Eastern Tasmania bioregions presented in Chapter 3) anglers may choose to increase their effort to target novel species or financially invest in the fishery (van Putten *et al.* 2017).

While this thesis considers future changes in temporal habitat off eastern Australia, the social implications of these changes are likely to be most challenging for seafood-dependent communities within developing nations. For example, the deployment of near-shore fish aggregations devices (FADs) off island nations throughout the South Pacific is an initiative aimed at increasing food security through aggerating pelagic fish and increasing their supply to rural communities (Albert *et al.* 2014; Bell *et al.* 2009). However, the distributions of target species are dynamic and seasonally variable (Hobday *et al.* 2011a), indicating that climate-driven changes to environmental conditions may alter their interactions with FADs and the subsequent availability to seafood-dependent communities. While impacts could be positive (increased temporal persistence of target species) or negative (declines in persistence), future projections of the persistence of suitable environmental conditions (e.g. days per season or months per year) throughout regions where FADs are deployed could aid affected communities. For example, it is foreseeable that government and NGO investments in future

food security through the provision of gear and subsidised fuel cost to support fishing, or through land tax exemptions to support the growth of subsistence agriculture, could be informed by forecast of the likely future availability of fishery species. While the data and models presented in this thesis are specific to kingfish from eastern Australia, the methods (e.g. environmental habitat modelling using citizen science data and measuring distribution changes while accounting for sources of natural climate variability) and ideas (e.g. temporal habitat persistence as a proxy for fishing opportunity) presented are globally applicable. Similar work undertaken in other global marine climate change hotspots that are adjacent to societies that are more vulnerable than Australia's (Hobday and Pecl 2014; Pecl *et al.* 2014b) would provide increased scope to discuss the socioeconomic implications of changing pelagic fish distributions in more specific detail.

6.2 Beyond species occurrence as a response to environmental variation

Species' physiological responses are predicted to vary with respect to environmental conditions (Del Raye and Weng 2015), yet there remains a paucity of quantitative comparisons using data collected in the field. The species distribution modelling literature provides a wealth of evidence indicating that species presence and absence correlates with environmental variables (Elith and Leathwick 2009). However, presence-absence data are a biologically coarse measure of a species response to its environment and more sensitive responses (e.g. proximate composition indices or body condition measurements) may provide an increasingly detailed understanding of species responses to environmental conditions in the wild. This could occur when a species is present in areas of both marginal and optimal habitat quality but physiological indices measured on individuals from areas of marginal environmental habitat quality may be relatively poor compared to individuals from areas of optimal habitat. For

example, bottom temperature is known to be a significant predictor of not only the occurrence of Atlantic cod (*Gadus morhua*) but also of spatial variation in the growth and recruitment among spatially explicit stocks (Rätz and Lloret 2003). Similarly, sea surface temperature is correlated with the body condition for multiple small pelagic species from the western Mediterranean and Gulf of Mexico (Adams *et al.* 2018; Brosset *et al.* 2015). Detecting species physiological responses to environmental variables can have important applications, particularly for species of high conservation value or those targeted in fisheries, as these relationships can, for example, help explain variation between spawning stock biomass and subsequent recruitment (Morgan *et al.* 2011). These relationships may also have important implications for seafood industries if physiological indices related to seafood quality are found to correlate with climate change affected environmental variables (Coleman *et al.* 2019).

While previous research has compared physiological responses to single environmental variables (e.g. temperature; Brosset *et al*. 2015), this thesis demonstrates that habitat suitability models are valuable for this application because of their capacity to incorporate species' preferences for multiple environmental covariates (Waltari *et al.* 2014). This approach allowed field-derived measurements of the physiological status of kingfish body condition (considered as an integrated measure of physiological status) to be simultaneously compared to the suite of variables that are known to significant predictors of environmental habitat suitability (Chapter 5). It is likely that the inclusion of multiple significant predictors of kingfish environmental habitat improved the variance explained among body condition data that are presented in Chapter 5. This idea could be tested using the data contained in this thesis by comparing the variation explained in kingfish body condition data by temperature-only thermal habitat suitability estimates and environmental habitat suitability estimates that include multiple variables (as done in Chapter 5). By integrating data describing the physiological status of

kingfish with estimates of environmental habitat suitably, Chapter 5 of this thesis extends the application of multiple variable habitat models for spatially differentiating between individuals in relatively good or poor body condition.

Moving beyond species occurrence as a response to environmental variation to consider underlying physiological responses can also be used to address questions surrounding climate-driven species redistributions. For example, are individuals that extend beyond their historic range boundaries in poor condition due to the presence of suboptimal environmental suitability in novel habitats? Or are individuals that extend beyond their historic range boundaries capable of doing so because they are in peak physiological condition and can tolerate suboptimal conditions? In this context, the relationship between kingfish body condition and spatiotemporally variable environmental quality (identified in Chapter 5) provided a physiological explanation of the highly seasonal occurrence and poleward extension of this species' range edge in Tasmania's coastal ocean (identified in Chapter 2). Taken together, these chapters suggest that kingfish in south-eastern Australia follow the annual poleward advance and equatorward retreat of suitable oceanographic habitat due partly to the effects of changing environmental conditions on body condition. Future oceanographic conditions predicted for eastern Australia (Hobday and Lough 2011) are therefore likely to support the persistence of kingfish, and other similarly affected coastal-pelagic fishes (Hill *et al.* 2015; Hobday 2010; Robinson *et al.* 2015b), in high quality condition at higher latitudes. Given that fecundity is known to covary with body condition (Rätz and Lloret 2003), changes to the distribution of fish in 'good' condition due to climate-driven environmental change has important implications for the abundance of spawning individuals in novel environments (Ling *et al.* 2009). The establishment of reproductive populations is a crucial step in the range extension

pathway (Bates *et al.* 2014) and the spatial redistribution of individuals with relatively high reproductive output is likely to expedite this process.

6.3 Role of citizen science in assessing climate-driven change

This thesis highlights the value and utility of citizen science data for quantifying species environmental habitat preferences. The proliferation of citizen science programs in recent years (Pecl *et al.* 2019; Silvertown 2009) is providing increased opportunity to understand the environmental associations of large suites of species, including those that have traditionally been difficult to sample (e.g. large pelagic fishes or cryptic reef-associated species). Subsequently, researchers have never been better equipped to model species distributions (e.g. Brodie *et al*. 2018), which is timely given that the physical effects of climate change are currently driving a global redistribution of biodiversity (Pecl *et al.* 2017) and responding to these changes is crucial for society (Bonebrake *et al.* 2018). For example, citizen science data have been a valuable resource that has contributed to our present understanding of a globally coherent fingerprint of climate change impacts across terrestrial (Parmesan and Yohe 2003) and marine systems (Poloczanska *et al.* 2013). Increasing access to large datasets that describe species occurrences in space and time also present opportunities to further our understanding of how environmental variables shape species distributions and ecologies, which has remained a key research question for over 150 years (Darwin 1859). For example, Payne *et al.* (2016) compared thermal preferences for tropical and temperate fishes with the temperature of their warm range boundaries, determined using citizen science occurrence records, to show that the thermal optima for tropical fishes is more closely correlated with their warm range boundary than for temperate fishes.

6.4 Future directions

Numerous opportunities for strategically quantifying species-environment relationships for the purpose of detecting and adapting to climate change have emerged through the research contained in this thesis and considering its place in the broader literature. It is evident that there is great value in continuing to use and apply data from citizen science programs, however these data must be used in a way that is fit for purpose (Dickinson *et al.* 2010). A key challenge for species redistribution science is identifying species geographic boundaries (e.g. 'core distribution' or the 'range edge') in order to measure how these are responding to the physical effects of climate change. Although the majority of range-shift assessments utilise species distribution models (Bonebrake *et al.* 2018), which commonly predict the distribution of suitable environmental conditions for a species and not the distribution of a species *per se*, there is no standard convention for determining threshold suitably values that relate to the core or edge of a species distribution (Liu *et al.* 2005). For example, A threshold of 0.5 is widely used in ecology (Bailey *et al.* 2002; Manel *et al.* 1999; Stockwell and Peterson 2002) to convert continuous projections (i.e. on a 0 – 1 scale) of environmental habitat quality into binary outputs, despite often being an arbitrary selection lacking ecological basis (Liu *et al.* 2005). Citizen science holds potential for providing a data-driven approach to identify suitability thresholds that are relevant to species core or range edge distributions, particularly where citizen science initiatives specifically aim to record observations for species' core or range edge distributions (e.g. Redmap Australia; www.redmap.org.au). Meaningful estimates of species range change can be derived, provided the environmental suitability threshold value (determined through comparisons with citizen science data) used to characterise a species' distribution is held constant over the study period (e.g. the range shift analysis contained in Chapter 2). Adopting this approach for determining

and measuring changes in species distributions with commonly used species distribution modelling methods could improve the agreement between observed and predicted range-shifts and the interpretability of results.

Given that kingfish off eastern Australia are a focal species for an established, government administered, tagging program, future research could benefit from utilising existing relationships with anglers to deploy a small number of satellite tags. The deployment of satellite tags would facilitate comparisons between projections of suitable kingfish oceanographic habitat presented herein with known animal movement and activity. These comparisons would be useful for validating and refining kingfish habitat models and for addressing key questions around the realised temporal persistence of this key target species in high-latitude bioregions off south-eastern Australia. Activity data may also provide novel insights into whether or not individuals from high-quality oceanographic habitat are more active than fish located in suboptimal habitat. This comparison has the potential to generate supporting lines of evidence for the results presented in Chapter 5 (e.g. are kingfish from optimal oceanographic conditions are in better condition *and* more active?) or generate a new research questions surrounding the fitness of climate-driven vagrants (e.g. are vagrant individuals in better condition and more active than the population average, and thus more biological equip to shift into novel environments?).

Identifying physiological indices that correlate with seafood quality and assessing whether these respond to environmental heterogeneity is an emerging area of climate impact detection (Coleman *et al.* 2019). While the results of Chapter 5 demonstrate that the body condition of kingfish off eastern Australia is positively related to environmental habitat quality, it remains unknown if kingfish condition (i.e. phase angle measurements taken using bioelectrical

impedance analysis) correlates with the seafood quality of this species. This is a necessary future step before links are drawn between oceanographic habitat suitability and the spatial distribution of kingfish seafood quality off eastern Australia and implications for market value of kingfish are discussed. Future research investigating environmental effects on the physiology of fishery target species could increase the relevance of their results to the seafood industry by measuring responses that are known to reflect seafood quality. For example, response variables could include lipid composition or fatty acid profiles (e.g. Coleman *et al*. 2019), which are routinely assayed in biochemistry laboratories for a reasonable price ($50 - $80 AUD per sample; pers. comm.). Analyses such as these could form the science-base of discussions around the effects of rapidly changing environmental conditions on seafood market value, which is an area of research that cuts across ecological, social and economic dimensions. From an ecological perspective, intense, short-term anomalous events such as marine heatwaves could provide opportunities to quantify relationships between environmental conditions and physiological indices that reflect seafood quality in the field. The results of Chapter 5 demonstrate that kingfish condition was related to environmental habitat quality at lead-times up to 4 weeks prior to measurement. Therefore, it is foreseeable that tissue samples from fishery target species taken prior to the development of a marine heatwave and repeatedly throughout the duration of these events could be used to address questions surrounding the effects of environmental heterogeneity on seafood quality in a field setting.

The rapid rates of climate-driven species redistributions reported globally are genuinely concerning and challenge human adaptive capacity (Bonebrake *et al.* 2018; Pecl *et al.* 2017; Poloczanska *et al.* 2013). For example, based on the finding of Chapter 2, the poleward edge of suitable habitat for kingfish off eastern Australia is likely to have shifted poleward by approximately 41 km during the time it has taken to complete this thesis (i.e. 3.8 years). In

many instances, it will not be possible to derive quantitative analyses of species-environment relationships like those presented herein to support climate change adaptation due to, for example, a paucity of data or a lack of dedicated scientific research programs. Regardless, human adaptation strategies are urgently required to minimise losses and maximise opportunities associated with the global redistribution of biodiversity. Alternative data sources and knowledge systems have enormous potential to underpin adaptation strategies and may be better equipped at keeping pace with the biological effects of climate change than highly quantitative and time-consuming single species approaches. For example, recent comparisons have demonstrated that traditional knowledge and expert opinion often converges with projections from species distribution models (Lopes *et al.* 2018; Mason *et al.* 2019). Future research is required to further test the accuracy of traditional knowledge and expert opinion for determining species-environment relationships, and to justify the value of this promising approach to policy-makers. Importantly, expert knowledge should be collected in a formalised way to ensure that information relating to species responses along environmental gradients are accurately collected by researchers. Multi-criteria decision analysis is one methodological option that is likely to be appropriate for this application given that it allows for the collection and synthesis of disparate data sources, including expert opinion, and has been previously applied to assess species climate vulnerability (Kim and Chung 2013). Ultimately, the consideration of disparate data sources from diverse knowledge systems will be crucial to ensuring that human adaptive capacity can keep pace with biological responses to a rapidly changing global climate system.

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The referencing style adhered to throughout this thesis conforms to the standards of the journal Marine and Freshwater Research.

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